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PROCEEDINGS OF A SYMPOSIUM

Biotic Stress of Barley

In Arid and Semi-Arid Environments



Huntley Lodge, Big Sky, Montana, July 31-August 2, 1990



BEST AVAILABLE DOCUMENT

PROCEEDINGS
*of the International
Symposium on
Biotic Stress of Barley
in Arid and
Semi-Arid Environments*

**Huntley Lodge
Big Sky, Montana**

Presented by
The Department of Plant Pathology
Montana State University
Bozeman, Montana
and
The International Center for Agricultural
Research in Dry Areas (ICARDA)
Aleppo, Syria

July 30 - August 2, 1990

Preface

The International Symposium on *Biotic Stress of Barley in Arid and Semi-Arid Environments* was held in Big Sky, Montana from July 30th through August 2nd, 1990. The symposium was a culmination of a cooperative agreement linking USAID, ICARDA (International Center for Agricultural Research in Dry Areas), and Montana State University. The agreement and subsequent symposium addressed the role of biotic stresses in barley and methods of prevention.

These proceedings consist of reports which were presented at the symposium to further the exchange of ideas and information among research workers. Consequently, responsibility for statements rests with the author(s). Before quoting any statements, the author(s) involved should be contacted.

To the authors and to all others who contributed to the success of this symposium, the planning committee extends its appreciation.

Jack Riesselman
Planning Committee Chairman

Symposium Agenda and Speakers

SESSION I — INTRODUCTION

Tuesday, July 31 (Morning Session)

- 8:15-8:30 *Introductory Remarks*
Dr. Russell Muntifering
Associate Director
Agricultural Experiment Station
Montana State University
Bozeman, Montana
- 8:30-8:45 *Opening Remarks*
Dr. Jit Srivastava
Deputy Director General for International Cooperation
ICARDA
Aleppa, Syria
- 8:45-9:15 *Keynote Address:*
Foreign Agricultural Assistance and American Producers
Dr. Lynn L. Pesson
Executive Director for BIFAD
Board of International Food and Agricultural Development
Washington, D.C.
- 9:15-9:45 *Lessons from History*
Dr. Jack R. Harlan
Professor Emeritus
University of Illinois
Urbana, Illinois
- 10:00-10:40 *Methods Used in Transferring Technology from the Laboratory to the Producer: Economic Considerations*
Dr. G. Edward Schuh
Dean, Hubert H. Humphrey Institute of Public Affairs
University of Minnesota
St. Paul, Minnesota
- 10:40-11:20 *Transferring and Understanding New Technology: Sociological Implications*
Dr. Keith Jamtgaard
Department of Sociology
Montana State University
Bozeman, Montana

11:20-noon *Global Status of Barley and Its Constraints*

Dr. D. H. B. Sparrow
Department of Agronomy
The University of Adelaide
Glen Osmond, South Australia

SESSION II — INFLUENCES OF STRESS ON BARLEY PRODUCTION

Tuesday, July 31 (Afternoon Session)

- 1:00-1:40 *Future of Barley in a Global Context*
Dr. Mel Anderson
Vice President & General Manager
Anheuser-Busch Resources, Inc.
St. Louis, Missouri
- 1:40-2:20 *Roles of Barley Diseases in Arid and Semi-Arid Environments*
Dr. Eugene L. Sharp
Professor Emeritus
Department of Plant Pathology
Montana State University
Bozeman, Montana
- 2:20-3:00 *The Influence of Water Potential on Plant-Microbe Interactions*
Dr. Laszlo N. Csonka
Department of Biological Sciences
Purdue University
West Lafayette, Indiana
- 3:20-4:00 *Stability of Stress Resistance to Biotic and Abiotic Stress Factors*
Dr. J. E. Parlevliet
Plant Breeding Department
Agricultural University
Wageningen, The Netherlands
- 4:00-4:40 *Roles of Abiotic Stress in the Development of Foliar Diseases*
Dr. Roy D. Wilcoxson
Department of Plant Pathology
University of Minnesota
St. Paul, Minnesota

SESSION III — INFLUENCES OF BIOTIC STRESS ON BARLEY PRODUCTION

Wednesday, August 1 (Morning Session)

- 8:00-8:40 *Soil-Borne Pathogens as Components of Plant Stress*
Dr. Robert L. Conner
Agriculture Canada Research Station
Lethbridge, Alberta, Canada
- 8:40-9:20 *The Role of Stress on Plant and Insect Interactions*
Dr. Elvis A. Heinrichs
Department of Entomology
Agricultural Center
Louisiana State University
Baton Rouge, Louisiana
- 9:20-10:00 *Influences of Biotic Stress on Barley Production: Interactions Between Diseases and Drought*
Dr. Peter G. Ayres
Division of Biological Sciences
Institute of Environmental & Biological Sciences
University of Lancaster
Lancaster, United Kingdom
- 10:20-11:00 *Modeling Crop Response to Growth Reducing Factors*
Dr. W. van der Werf
Department of Theoretical Production Ecology
Wageningen Agricultural University
Wageningen, The Netherlands
- 11:00-11:30 *Influence of Mycorrhizae on Barley in Arid Environments*
Dr. William E. Grey
Department of Plant Pathology
Montana State University
Bozeman, Montana
- 11:30-12:00 *Effects of Stress on the Etiology of Barley Yellow Dwarf Virus*
Dr. André Comeau
Agriculture Canada
Ste-Foy, Québec, Canada

SESSION IV — BREEDING METHODOLOGIES

Wednesday, August 1 (Afternoon Session)

- 1:00-1:40 *Classical vs. Recurrent Selection Breeding Approaches for Developing Disease Resistance*
Dr. R. Thomas Ramage
USDA, ARS
Department of Plant Sciences
University of Arizona
Tucson, Arizona
- 1:40-2:20 *Molecular and Energetic Aspects of Induced Resistance in Barley*
Dr. Viggo Smedegaard-Petersen
Plant Pathology Section, Department of Plant Pathology
The Royal Veterinary & Agricultural University
Copenhagen, Denmark
- 2:20-3:00 *Recombinant Inbred and Doubled Haploid Lines: The Biology, Technology, and Utility*
Dr. Patrick M. Hayes
Department of Crop & Soil Science
Oregon State University
Corvallis, Oregon
- 3:20-4:00 *Using Genetics in Barley Breeding*
Dr. Thomas K. Blake
Department of Plant & Soil Sciences
Montana State University
Bozeman, Montana
- 4:00-4:40 *Potential for Transformation in Barley*
Dr. David A. Somers
Department of Agronomy & Plant Genetics
Plant Molecular Genetics Institute
University of Minnesota
St. Paul, Minnesota

SESSION V — TRANSFERRING THE TECHNOLOGY

Thursday, August 2 (Morning Session)

8:00-8:30 *Montana-USAID Activities in Developing Barley Germplasm*

Dr. Michael E. Bjarko

Barley Breeder

Busch Agricultural Resources, Inc.
Fort Collins, Colorado

8:30-9:00 *ICARDA Activities in Developing Barley Germplasm*

Dr. Salvatore Ceccarelli

ICARDA

Aleppo, Syria

9:00-9:40 *Subsistence Farmer Strategies in Response to Drought and Biotic Stress Uncertainty*

Joop A. G. van Leur

ICARDA

Aleppo, Syria

10:00-10:30 *Successes in Transferring Technology Within Developing Countries*

Dr. Amor H. Yahyaoui

Director, Ecole Supérieure d'Agriculture
du Kef

Kef, Tunisia

10:30-11:00 *Future of Landraces*

Dr. Rebecca McGee

Department of Plant Pathology
Montana State University

Bozeman, Montana

Dr. Stephanía Grando

ICARDA

Aleppo, Syria

11:00

Where Do We Go From Here? — Future Directions

Dr. William R. Furtick

Agency Director for Food & Agriculture
Bureau for Science and Technology

U.S. Agency for International Development (USAID)

Washington, D.C.

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UTILIZATION OF BARLEY LANDRACES IN A BREEDING PROGRAM

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Introduction

Barley evolved in West Asia, where it has been grown since the beginning of settled agriculture (Harlan, 1975a). The area is characterized by abiotic stresses such as drought, cold, heat, and salinity. This, together with low soil fertility and low input practices of traditional agriculture results in low productivity. Barley is the predominant crop in this region, farmers use it primarily as animal feed and utilize both the grain and the straw (Ceccarelli, 1984; Ceccarelli *et al.*, 1987). Landraces are still widely grown in many of these areas. Farmers value their stability of performances, feeding quality and productivity. Additionally, it has proven to be difficult to outyield them with modern cultivars. Landraces are the dynamic product of millennia of complex interactions of natural and artificial selection, isolation and migration and seed exchanges. They have been tested by time and are adapted to a localized area. Selection pressures were exerted for hardiness and dependability, rather than high productivity. As Harlan (1975b) points out:

'Land races have a certain genetic integrity. They are recognizable morphologically; farmers have names for them and different land races are understood to differ in adaptation to soil type, time of seeding, date of maturity, height, nutritive value, use and other properties. Most important, they are genetically diverse. Such balanced populations - variable, in equilibrium with both environment and pathogens, and genetically dynamic - are our heritage from past generations of cultivators.'

The genetic variability of landraces provides an insurance against hazards. A landrace usually yields something, despite the sometimes extreme biotic and abiotic stresses it encounters in the majority of the years. In traditional agricultural system, high yields have never been necessary, but dependability is. Landraces may not yield much by our modern standards, but they do yield something and will keep the farmer alive until next crop.



Although landraces were not selected primarily for high productivity, they were not selected solely for survival. They may contain high producing components as evidenced by the selection from landraces of our first advanced cultivars at the turn of the century (Frankel and Soule', 1981). Until about 50 years ago landraces were the primary sources of material for genetic improvement. At that time, they started being replaced by modern cultivars, unfortunately before their potential had been fully explored and/or exploited. Many, if not most, breeders concentrated on the use of superior lines derived from landraces resulting in an erosion of the adapted germplasm. This erosion has two facets: the use of relatively few parents with the concomitant reduction in genetic diversity and the replacement of landrace populations before they could be collected, assessed, and conserved in germplasm banks. This narrowing of the genetic base has been a common feature of many plant breeding programs and has been accompanied by a trend towards homogeneity: one clone, one pure line, one hybrid (Simmonds, 1983). A very common attitude of modern breeders is to neglect locally adapted germplasm on the base that it is susceptible to biotic stresses, mainly diseases, and it has a low yield potential. While this is to a large extent true when landraces are evaluated as populations, and when they are grown under optimum climatic and edaphic conditions, it is no longer necessarily true when individual genotypes extracted from landraces are evaluated (Ceccarelli et al., 1987; van Leur et al., 1989).

Use of barley landraces at ICARDA

The major objectives of both the ICARDA barley breeding project for low rainfall areas and the MSU-USAID barley project have been to increase yield stability by decreasing the frequency of crop failure. The environments of West Asia and North Africa (WANA region) are characterized by low yields due to unpredictable variability of the frequency, timing, severity, and duration of abiotic stresses. The low yields are predictable, their causes are not. When working in arid and semi-arid areas where adapted germplasm (both landraces and wild progenitor i.e. Hordeum spontaneum) is available, its incorporation into the breeding program may be central to the success of the program (Ceccarelli, 1984; Ceccarelli and Mekni, 1985).

Landraces were not used in a systematic fashion in the ICARDA barley breeding project until 1984 (Ceccarelli, 1984), although preliminary data on a very small sample from an extensive collection of material from Syria and Jordan (Weltzien, 1982) were extremely promising. The procedure for utilizing the material of this collection was first to assess the amount of genetic variation for agronomic and morphological characteristics and secondly to determine the extent of genetic diversity within the landraces that was useful for breeding purposes. Attention was focused primarily on Arabi Abiad and Arabi Aswad - the two barley landraces widely grown in Syria.

In 1984-85 single-head progenies were evaluated for agronomic, morphological, and quality characteristics as well as for resistance to several diseases. A large and useful amount of genetic variation was found both within and between populations for a large number of traits (Ceccarelli et al., 1987; van Leur et al., 1989). The next question was how to utilize it. The role of landraces in a breeding program falls into two broad categories: 1. utilization as donor of genetic material; 2. utilization as source of information which can help us to answer some questions central to adaptation.

1. Landraces as donor of genetic material

There are different ways by which landraces can be utilized as donors of genetic material. The first and by far the fastest and the cheapest is simply the pure line selection within landraces. An example of the potential of this approach is given by Tadmor, a pure line that was selected out of Arabi Aswad, the black seeded Syrian landrace. Tadmor has been tested together with Arabi Aswad over a period of four years (from 1985/86 to 1988/89) in on-farm trials at 25 locations in areas of Syria receiving less than 250 mm annual rainfall (long term average). At 18 locations Tadmor outyielded Arabi Aswad by an average of 9%. At the other seven locations, although the original landrace outyielded Tadmor, it had an average advantage of only 4.4% (Table 1).

Although Tadmor and other lines selected from landraces have clearly shown the effectiveness of the method, pure line selection should only be used for short term goals as it has a serious drawback that may be inadvertent. When superior pure lines are extracted from a landrace and released as new varieties, the landrace is often lost as farmers adopt the new pure line variety. The replacement of the local variety (very often a mixture of many genotypes) with a pure line results in a dramatic narrowing of the genetic variation with consequent loss of genetic resources for future needs. In addition pure lines are probably not the most suitable type of cultivar in the long term for the arid and semi-arid environments. In fact adaptation, and thus stability of performance, to adverse and variable conditions is likely to be associated with genetic heterogeneity, even though the level of heterogeneity has not to be as complex as it is in the original population.

Varietal improvement based on the use of landraces as parents in crosses is impressive in many crops, many landraces have contributed to yield increases (Chang, 1985) although mostly through transferring of genes for disease and pest resistances. This is perhaps one of the most common use of landraces today and in the recent past - breeders will routinely look to the germplasm banks and world collections for sources of resistance to diseases and pests. Several examples can support the need for genetic conservation, but landraces can play a major role as donors of genetic components like adaptation.

Another way in which landraces can be incorporated in a breeding program as sources of genetic material is to create mixtures of superior lines extracted from landraces.

While the first two approaches have been implemented and fully incorporated in the barley breeding program at ICARDA, the role of genetic heterogeneity is still under testing. To generate information on what is the best compromise between the complexity of mixtures and stability of higher yields, three mixtures at different levels of complexity (4, 8 and 16 lines) were evaluated along with the single components (pure lines), for three years in a total of 11 location/year combinations (Table 2).

Two different techniques have been used to measure stability: the joint regression analysis and a non parametric method proposed by Nachit and Ketata (1986).

Over 11 environments (Table 3) only the mixture of 4 lines had a better rank (12.8) and a lower standard deviation of ranks (5.9) than the local cultivar Arabi Aswad ($R = 13.5$, $SDR = 6.9$). Furthermore the mixture of 4 lines showed a better response ($b = 0.90$) and a higher intercept ($a = 168.7$) than A. Aswad ($b = 0.85$, $a = 160.1$).

Out of the three best lines (shown at bottom of Table 3) in terms of average rank, only two (SLB 42-64 and SLB 45-93) performed consistently well across the environments.

Incorporating landraces in a breeding program in any of the above three scenarios requires identifying superior lines. When the target environment is a stress environment with adverse and variable conditions, Ceccarelli and Grando (1989) reported that in barley the efficiency of direct selection under stress conditions is higher than the efficiency of indirect selection. The efficiency of selection increases even more when direct selection is applied on lines extracted from landraces. This indicates that to fully exploit the usefulness of landraces in barley breeding for stress conditions, testing and selection have to be conducted under the target conditions where adapted germplasm can fully show its advantages.

2. Landraces as source of information

The second major way in which landraces can be utilized in breeding, physiology and genetics research is as a source of information. Landraces can be extremely useful tools to investigate both the genetic and morphological mechanisms enhancing stability in stress environments. The two major genetic mechanisms enhancing stability are individual buffering and population buffering (Allard and Bradshaw, 1964). While the individual buffering can be largely associated with heterozygosity, population buffering is a mechanism of stability associated with genetic heterogeneity.

2

There is abundant evidence that landraces are mixture of genotypes, but a direct relation between genetic heterogeneity and stability has yet to be proven. It is not unreasonable to speculate, however, that after millennia of natural and artificial selection, the genetic structure of landraces must confer some advantages and is not an accidental product of evolution. Natural selection has failed to identify a single superior genotype. Rather, natural and artificial selection has molded landraces into being an architecture of genotypes with different combinations of traits.

Table 4 compares morphological and developmental traits of improved cultivars and of lines extracted from Syrian and Jordanian landraces. The Syrian material has a higher frequency of genotypes with prostrate or semi-prostrate growth habit, cold tolerance and short grain filling period. Lines from Syria had a lower frequency of types with good growth vigour and early heading. This combination of traits in the Syrian landraces allows these populations to escape adverse drought conditions (short grain filling period) at the end of the season and to avoid frost threats (prostrate growth habit and cold tolerance). The Jordanian material does not encounter such environmental extremes and possess a combination of morphological traits which adapt it to mild temperatures during the growing period.

In addition to a high frequency of certain combinations of traits, landraces have another powerful adaptive mechanism - a substantial amount of variability within the population for each of these traits. Figures 1, 2 and 3 show the variability within Syrian and Jordanian landraces and improved cultivars for cold damage, days to heading and yield under drought conditions. This distribution of levels of the individual traits in conjunction with combination of traits, allows a landrace as a whole to finely tuned itself and respond to the unpredictable and variable environmental conditions it may encounter each crop cycle. In Table 5, lines from a Syria landrace are classified by early growth vigour and growth habit. There are some combinations which are never represented (i.e. poor early growth vigour and semi-prostrate or prostrate growth habit). The highest frequency of genotypes have intermediate early vigour and are semi-prostrate to prostrate. These types are slightly more cold tolerant and later in heading than types with good early vigour. However, because of a short grain filling period, they are better equipped to escape terminal drought. Other combinations, provide high levels of cold tolerance with poor early growth vigour, very prostrate growth habit and late heading. A small percent of genotypes with low levels of cold tolerance, early heading and long grain filling period will most probably be favoured in mild winters with no late spring frosts and less severe terminal stress.

A population with this architecture of genotypes will be able to respond to many fluctuations in its environment. Within the population some set of genotypes with some combinations of traits will allow the population to survive, if not thrive, in an unpredictable environment. The capability of adapting to

fluctuating environments that such an architecture of genotypes provides underlies the long term stability and the dependability of landraces.

Conclusions

The importance of locally adapted material for stressful environments has been recognized early at ICARDA and selections from landraces have been and are still used extensively in the breeding program. From landraces we can learn how to improve stability of yield in difficult and variable environments. They offer a genetic base for adaptation on which breeders can build new varieties.

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Table 1. Grain yield (kg/ha) of Tadmor and Arabi Aswad in on-farm verification trials in areas with less than 250 mm rainfall in Syria.

Number of locations	Tadmor	Arabi Aswad	Difference
18 (72%)	1728	1596	+ 9.0%
7 (28%)	1672	1746	- 4.4%

Table 2. Total rainfall (mm) and average grain yield (kg/ha) at each location/year combination.

Location	Year	Rainfall	Grain yield
Bouider	1986-87	176.2	61.2
Breda	1986-87	244.6	451.4
Tel Hadya	1986-87	357.9	1791.8
Bouider	1987-88	385.7	2826.7
Breda	1987-88	414.8	3379.7
Tel Hadya	1987-88	504.2	3743.8
Cyprus	1987-88	321.0	4806.1
Bouider	1988-89	186.4	596.2
Breda	1988-89	193.8	1328.1
Tel Hadya	1988-89	234.4	3275.0
Hassake	1988-89	184.5	1028.2

Table 3. Average grain yield (GY), regression coefficient (b), intercept (a), average ranking (R), and standard deviation of ranks (SDR) across 11 environments of 3 mixtures, 3 pure lines from landraces (SLB), and A. Aswad.

	GY (kg/ha)	b	a	R	SDR
Mixture 4 lines	2066.8	.90	168.7	12.8	5.9
Mixture 8 lines	1937.7	.90	24.1	16.0	6.2
Mixture 16 lines	2110.7	.99	15.4	11.7	7.8
SLB 42-64	2156.7	.99	64.0	9.0	6.8
SLB 45-93	2185.3	.99	146.5	8.8	4.3
SLB 45-58	2402.1	1.16	- 44.1	8.5	7.4
A. Aswad	1955.3	.85	160.1	13.5	6.9

Table 4. Mean of morphological and developmental traits of 1041 improved barley genotypes (unrelated to Syrian or Jordanian landraces) compared with 322 pure lines extracted from Syrian landraces and 232 pure lines from Jordanian landraces (from Ceccarelli *et al.*, in press).

Trait	Improved	Landraces	
		Syria	Jordan
Early vigour ¹	2.5	3.2	2.4
Growth habit ²	2.8	4.0	3.1
Cold tolerance ³	3.0	1.3	2.3
Days to heading	117.9	121.2	116.9
Grain filling	39.3	35.5	37.4
Yield potential	4398.0	3293.0	3947.0
Yield under drought	488.1	974.9	834.7

¹ Early vigour: 1=good, 5=poor.

² Growth habit: 1=erect, 5=prostrate.

³ Cold tolerance: 1=absence of damage, 5=leaf blades and sheaths yellow.

Table 5. Frequency of different combinations of early growth vigour (GV) and growth habit (GH), and mean values of cold tolerance (CT), days to heading (DH), and length of grain filling period (GF) in a sample of 321 lines of barley collected in the dry areas of Syria (from: Ceccarelli *et al.*, in press).

Combinations	%	GV ¹	GH ²	CT ³	DH	GF
Good vigour - Erect	0.0	-	-	-	-	-
Good vigour - Semi-prostrate	1.2	2.2	3.3	1.6	118.8	37.4
Good vigour - Prostrate	5.3	2.4	3.9	1.4	119.8	36.6
Int. vigour - Erect	0.0	-	-	-	-	-
Int. vigour - Semi-prostrate	6.2	2.9	3.4	1.5	119.7	35.8
Int. vigour - Prostrate	65.1	3.1	4.0	1.4	121.2	35.4
Poor vigour - Erect	0.0	-	-	-	-	-
Poor vigour - Semi-prostrate	0.0	-	-	-	-	-
Poor vigour - Prostrate	22.1	3.9	4.2	1.3	121.9	35.4

¹ Early vigour: 1=good, 5=poor.

² Growth habit: 1=erect, 5=prostrate.

³ Cold tolerance: 1=absence of damage, 5=leaf blades and sheaths yellow.

COLD DAMAGE

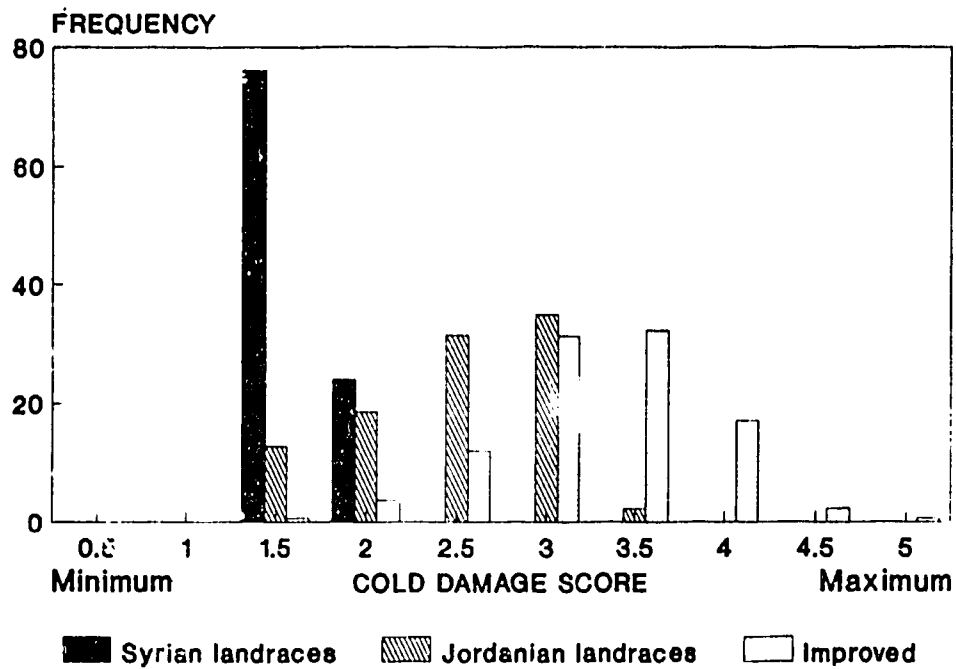


Figure 1. Variability within Syrian and Jordanian landraces and improved cultivars for cold damage.

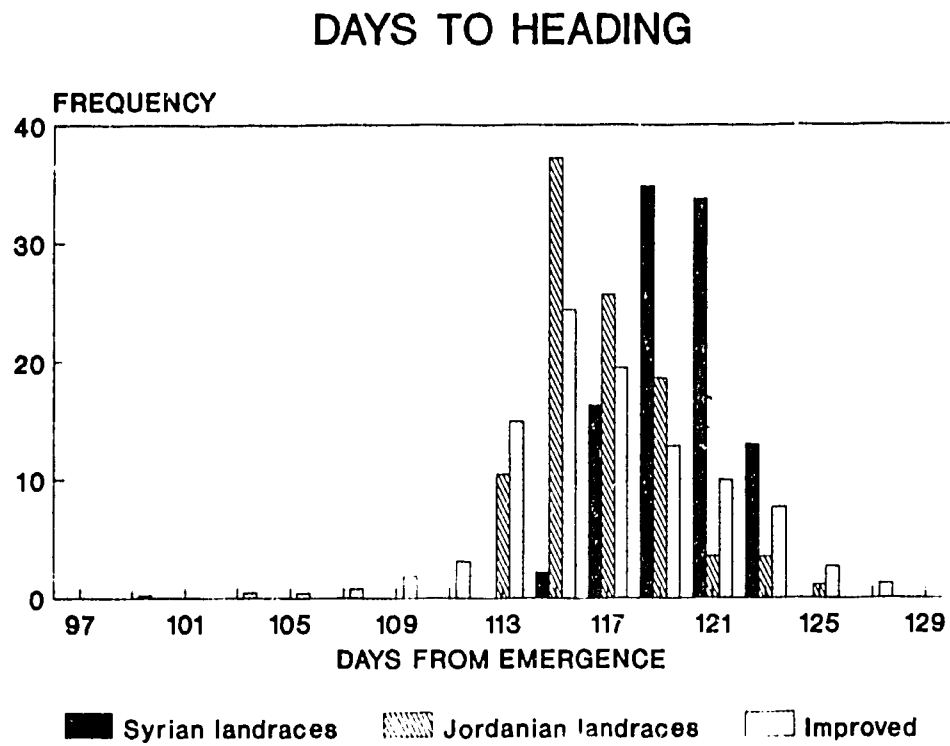


Figure 2. Variability within Syrian and Jordanian landraces and improved cultivars for days to heading.

YIELD UNDER DROUGHT

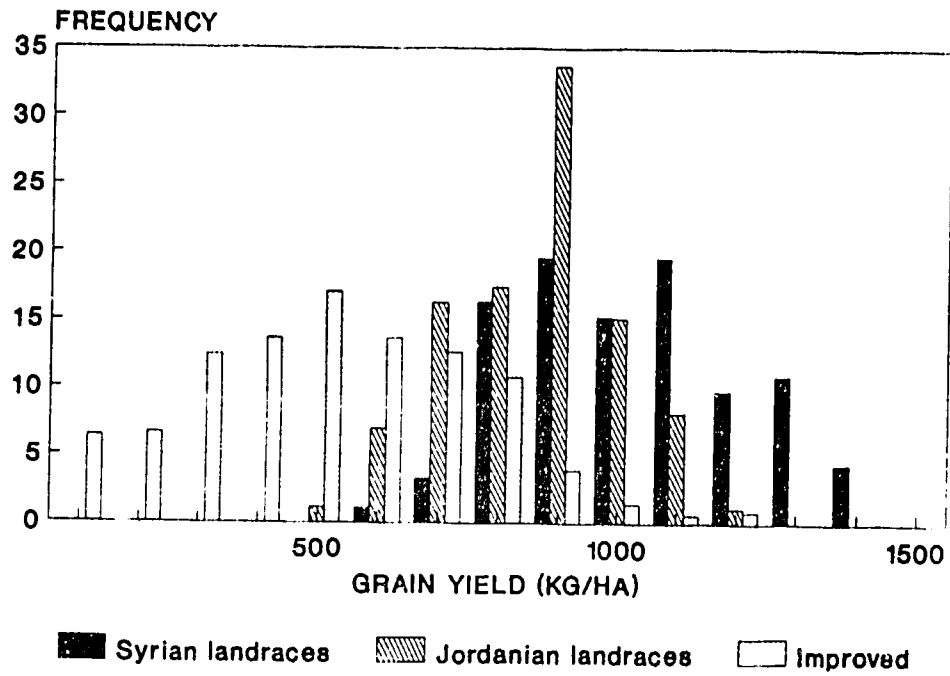


Figure 3. Variability within Syrian and Jordanian landraces and improved cultivars for grain yield under drought.

KEYNOTE ADDRESS

Foreign Agricultural Assistance and American Producers

Lynn L. Pesson*

The world in which we live is changing rapidly. There are manifestations of this all around us. The economic collapse of communism is perhaps our most striking example, but there are many more fundamental changes affecting our lives. The American farmer is part of it as well. In this presentation, I will look at the question of foreign agricultural assistance from three perspectives. First, I will focus on economic considerations, followed by a look at humanitarian concerns, and then a brief look at the technological situation.

Economics

There is a fundamental and inexorable change permeating everything we do. Whether we like it or not, we are fast becoming a global economy and an interdependent world, and this trend is accelerating. Although we remain the biggest player in the game, we no longer control it. To illustrate, at the end of World War II, the United States produced 50% of the world's gross national product; today it produces less than 30%. The next leading player in the current environment, Japan, produces roughly half that amount. So the name of the game now is trade, and trade is an international phenomenon.

I will illustrate the change occurring by presenting some agricultural data from 1988. In that year, the U.S. exported 76% of its wheat, 65% of its rice, 45% of its cotton, 41% of its soybeans, and 24% of its corn. Production from over one-third of our cropland was exported. Looking at this phenomenon from an economic perspective, we see that in 1978 the U.S. trade balance from agriculture was an \$8.2 billion surplus. We exported \$28.6 billion in agricultural products, and imported \$20.4 billion. Of the imports, \$6.6 billion was not competitive with U.S. products and \$13.8 billion was. It's a big ball game, and the competition is getting tougher all the time.

A friend of mine, who is a miller and shipper of rice, asserted at a meeting last year that although it was possible to ship rice from Louisiana to Tokyo cheaper than the Japanese can produce it, the Japanese will not let it in. This assertion is illustrative of a world-wide phenomenon of trade barriers of all sorts,

and the U.S. is no exception. Much of my family makes its living by producing sugar cane, so I have first-hand experience. I use this to illustrate that the world is full of trade barriers, but there is a rather strong world movement to reduce if not eliminate trade restrictions altogether. The result would be increased competition, which is part of the pattern of a global economy and an interdependent world.

What about the future of trade? This question is a major concern for farmers everywhere, and the U.S. is no exception. The U.S., Canada, and the European Economic Community have strong production capacities. Each is a surplus producer with a stagnant population.

Future market potential, consequently, is with the developing countries. Reports estimate there are 750 million people who live in a state of hunger. There are two problems in feeding them. They lack the wherewithal to purchase food, and there are difficulties in food distribution. Studies indicate, however, that if income is increased, 60% of the increase in income will go to food. Studies further indicate that as income increases, people diversify their diets. From coarse grains, they move to the more refined ones; as they move up the economic scale, their diets include more livestock products.

Additional data in this regard can be found in a study that compared fast- and slow-growth developing countries on the questions of imports and exports. With respect to exports from 1970 to 1984, the gap in level of exports between the faster-growth countries keeps growing larger, even during the period of the economic recession in the early 80s. The same pattern is apparent in the data for imports, but the gap between the fast- and the slow-growth countries was much larger. The implication is very strong. Those countries that grow faster trade more. From a self-interest standpoint, the data show that to stimulate trade, it is good business to help countries grow economically. East Asia is a case in point. Korea and Taiwan were helped by U.S. aid programs, and they are now two of our biggest customers.

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Humanitarian

There's another fundamental phenomenon operating out there. World population is growing at an accelerating rate. During this decade alone there will be 1 billion more mouths to feed — a 20% increase over the past decade. The world population will exceed 6 billion by the turn of the century, and demographers expect it to go to 10 billion by the middle of the next century. Some experts predict it will then begin to level off. The tough part of this problem is that there is a sharp dichotomy; most of the growth is taking place in the developing world. Sub-Saharan Africa, generally the poorest area in the developing world, is growing at a rate of more than 3% per year, for example. Agriculturists must ask several rather basic questions: Can we feed this many people? What about the problem in the developing world? For the moment we can do the job, but what will happen in 10 years? or 20? or 30?

I don't presume to have the answer. An assortment of experts more knowledgeable than I is needed to arrive at the answers. However, I would like to offer some points to ponder. Although surpluses exist, even in India, which was once thought to have an intractable food problem, there are signs that the so-called "green revolution" is leveling off. After a couple of decades of strong gains in yields, data from Asia indicate those yields are now plateauing, and in some instances are even declining. The breakthrough in rice hybridization by the Chinese may alter this course; but the challenge is dramatic for Asia, which has half the world's people to feed.

In order to further examine the yield question, we will look at a 1960-based index which projects data on the relationship among total grain production, area harvested, and yield. This index shows trends that are cause for concern. While area harvested has remained relatively steady, total production and yield have climbed steadily through 1986, almost doubling during the period. Total production and yield, however, have declined in the ensuing two-year period to 1988, and knowledgeable persons indicate the trend is continuing.

From this index, the same production data plotted against population growth show that from 1965 (roughly around the time the new miracle varieties began to reach farmers' fields) through 1986, production was growing faster than population. Since that time, we have lost ground, and if the trend continues, trouble could be on the horizon.

Viewed from another perspective, we see that population pressures on the environment are growing

rapidly. Signs are all around us; Eastern Europe is a striking example. Reports indicate that the disregard for the environment in the crumbling Soviet empire is overwhelming. It is symptomatic of what can happen if we aren't alert and responsive to the overall environmental problem. The challenge for agriculture is to become sustainable. Although we hear about the more obvious problems — water in dryland areas, the fragile lands, the depletion of forests — signs indicate that some intensive systems on productive soils are now coming under stress. Intensive rice culture in Asia, purportedly sustainable for thousands of years, is now coming under stress. The phenomenon of declining yields in Asia, mentioned earlier, may well be caused partially by the overuse of chemicals. It's a point to ponder.

Let me highlight the problem by using an illustration. One estimate showed that in 1975 there was approximately one acre of arable land in the world per person. If we accept this estimate, then by the year 2000 it is projected that there would be about .6 of an acre per person, a 40% drop in arable land availability per person. This vividly demonstrates the need for agriculturists to focus heavily on the two important considerations of resource sustainability and new technology. Presently, when agricultural research and technology transfer is under stress here and abroad for having done its job too well, it is imperative that we make the case to the public that dismantling the tremendous capacity we have built up is penny wise and pound foolish. This can best be accomplished by focusing on three objectives: providing resource sustainability in its broader context, ensuring new technology that maximizes production while maintaining or enhancing sustainability, and providing adequate economic incentives to the farmer to produce in a sustainable mode.

Technology

The U.S. no longer dominates the market for agricultural technology. A number of good institutions are located in Western world countries, and now there are also some good ones in the developing world. The International Agricultural Research Centers are now repositories of significant amounts of knowledge.

India, for example, now has more agricultural scientists than the U.S. However, they do have some second generation problems. Largely because of funding problems, their younger scientists are inbred, provincial, and out of touch with world science.

Looking back at my own experience in Malaysia, I find it epitomizes the change that has taken place in agricultural institutions. In 1966, when the Louisiana State University team arrived at the agricultural college, there were only 12 faculty, and the only Ph.D. was the new principal who had just returned from Leeds University in England. Today, Malaysia has more Ph.D.-level scientists than the agricultural complex from Louisiana which spawned them, and they now have better facilities and equipment.

It is crucial, therefore, for U.S. scientists to maintain contact with the world scientific community. A regular interchange is necessary for all concerned to keep abreast of the latest scientific information. There is increasing interest within the U.S. scientific community for collaborative relationships with other scientists on the international front.

Perhaps the best examples of international research networks are the Collaborative Research Support Programs of USAID. The eight CRSPs involve almost 900 scientists from 35 U.S. universities and 32 foreign countries. In their 10 years of existence, they have made numerous contributions to both foreign and U.S. producers, including injecting germplasm for needed characteristics in varieties of sorghum, millet, peanuts, beans and cowpeas. These characteristics include greater productivity, drought resistance, and insect, disease, and parasite resistance. Keep in mind that the CRSP programs are relatively young and they are just beginning to mature as research networks.

Germplasm is a key issue as illustrated by the accomplishments of the CRSP programs. Many U.S. varieties are the result of relatively homogeneous

gene pools. Much more heterogeneity is needed in the gene pools from which new varieties are developed. The best source of germplasm is the native habitat of plants. For example, corn came from Central America, soybeans from Asia, and wheat from the Middle East. To locate the source for genes with special characteristics, a good place to look is the native habitat. When the Louisiana rice crop was threatened by a new dread disease, Hoja Blanca, LSU scientists who were cooperating in the USAID rice program in Nicaragua isolated the gene in a native variety and transferred that gene into Louisiana varieties, saving producers untold millions of dollars.

The Future

There are three key points to make from this discussion:

- ▶ Future markets for U.S. producers exist in the developing world. Before these developing nations can trade with us, they need foreign exchange. Development programs must be designed to help them to help themselves grow economically.
- ▶ Population growth is putting increasing pressure on the world's resources. It's in everyone's interest to make the environment sustainable, and that includes agriculture.
- ▶ Technology is the key to the future. Cooperation and collaboration are crucial for scientific advancement. We no longer can do it alone.

FIGURE 1. Agricultural exports per capita:
Fast/slow growth groups (1970-1984).

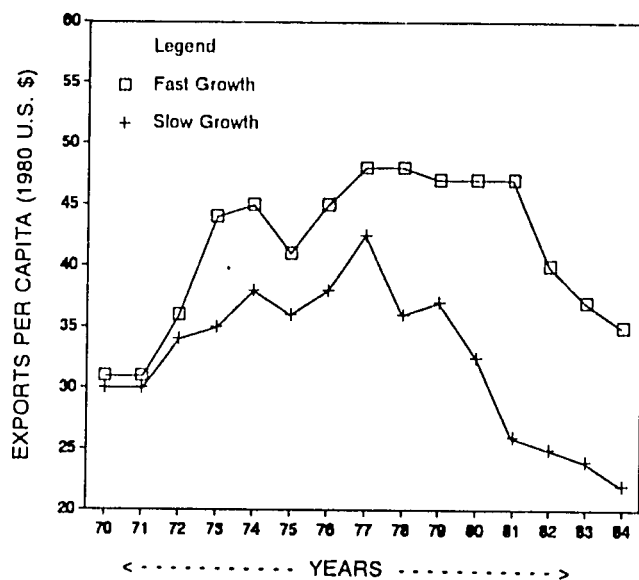


FIGURE 2. Grain production, area, and yield (1960-1988).

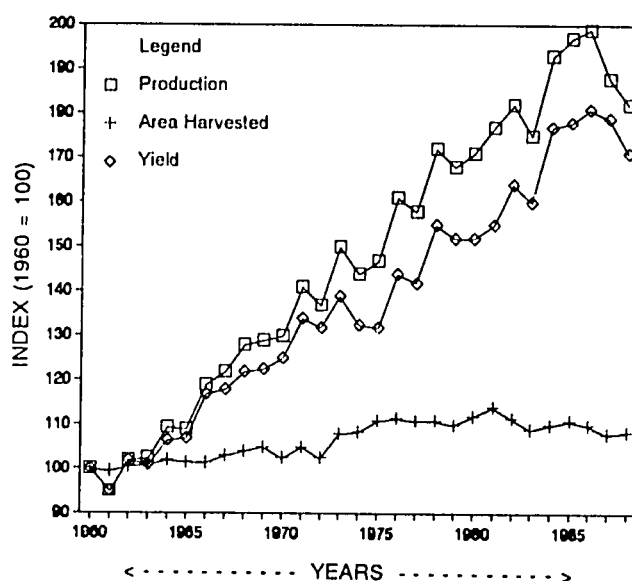


FIGURE 3. World population and grain production (1960-1988).

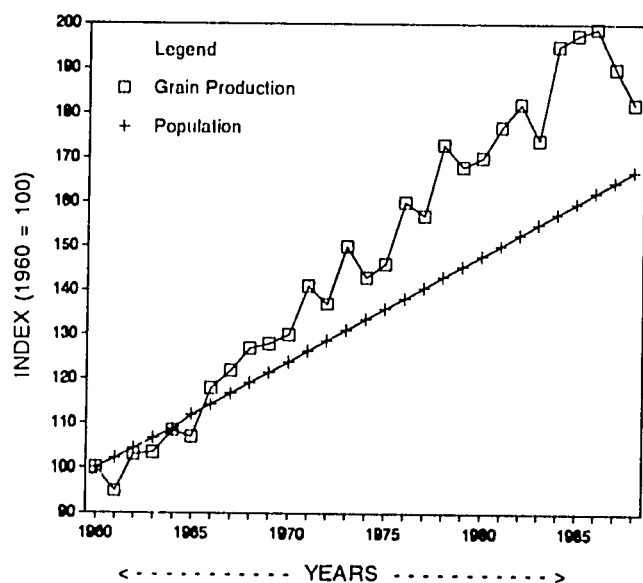
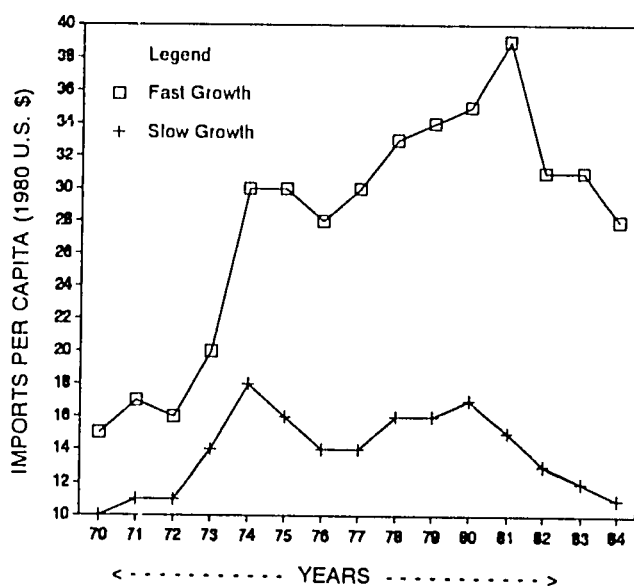


FIGURE 4. Agricultural imports per capita:
Fast/slow growth groups (1970-1984).



Lessons from History

Jack R. Harlan*

In this paper I shall try to update the latest information on origin and history of barley and describe some historical events of significance to agriculture.

The map (Figure 1) was published in *Science* (Harlan & Zohary, 1966), and has been reproduced and redrawn a number of times for different publications. Each dot can be verified by a collection, specimen, or citation in a trustworthy flora. We can now enlarge the range in both directions, since colonies have been located in Tibet and Morocco. Both the *spontaneum* and *agriocrithon* morphs were found in Tibet, and Chinese authors have claimed independent domestication in China. The same question was inevitably raised in view of the Moroccan finds. Isozyme studies have shown that the genetic patterns of these weedy African populations are different from the *spontaneums* of the Near East and do resemble cultivars grown in Morocco and southwestern Europe. This is suggestive of, but of course does not prove, independent domestication. There are other explanations for these patterns. Ultimately, these questions must be answered by archaeological evidence, but whenever a progenitor has a wide distribution, there are always possibilities for repeated domestications.

So far, the earliest evidence is concentrated in or near the Jordan Rift Valley. The current evidence is more precise than previous information. The earliest traces of food production in the Near East are found in Prepottery Neolithic A (PPNA). There is very little of it. The sites of Gesher, Netiv Hagdud, Gilgal, and Jericho, all within a radius of 15 km in the Jordan Valley, and Tell Aswan in the Damascus Basin are about all we have so far. For the time range, ca. 8000 B.C., some of the sites are rather large. Netiv Hagdud covers 1.5 ha and PPNA Jericho about 2.5 ha. All the early sites have remains of emmer wheat, and most, but not all, have barley. Cayonu, in Turkey, for example, ca. 7500 B.C., has not turned up barley, although I have collected wild barley on the site. All the early barleys were 2-rowed, like all the species in the genus (Zohary & Hopf, 1988).

In PPNB, a few centuries later, there are many more sites, and plant remains are more abundant. From then on, barley and emmer were inseparable

companions in the Neolithic expansion that spread through Europe and around the Mediterranean, eastward to the Indus and outward to Ethiopia. How it spread is now a subject of intense debate. Archaeology shows a clear temporal progression across Europe of about 1 km per year, but was it by farmers migrating or by hunter-gathers being converted and developing local farming systems? The debate is very lively at the moment, and we cannot go into that here, but suffice it to say that at one time barley may have been the most important crop in the world. For some of us it still is.

It must be admitted, from a culinary point of view, barley was seldom considered the classiest crop, but in classical times it was considered strong and nourishing. It was the ration of the soldier, the slave, and the gladiator. Pliny (trans. by Fackman, 1950) stated that gladiators were trained on it and were called "Hordiari," or "barley men." The people thought it was the strongest cereal, perhaps because if one could handle all that fiber, one would be strong, indeed. It is of interest that naked barley turned up very early in the archaeological record, by the 7th millennium B.C., or perhaps earlier.

Today, people who must consume a lot of barley tend to grow the naked kinds. Crossing high passes in the Himalayas, Karakorum, or Hindu Kush is a lesson in crop ecology. Going upslope, crop after crop drops out in orderly succession. The very highest villages attempting to survive by agriculture are usually reduced to barley and peas. It is not necessary to collect the barley to know that it is naked; you can hear it rustling in the wind. Naked barley can talk to you. The American Indians of both the Midwest and Southwest manipulated the rather trivial *Hordeum pusillum* to the point of developing naked sorts.

The Romans were wheat eaters from the foundation of the City, although Pliny stated that they ate emmer for the first 400 years. Bread wheat became popular after Alexander and increased the feasibility of large-scale export from North Africa (Harlan,

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1981). But the Greeks stubbornly stuck to their "maza," or barley porridge. Lawrence Angel, a physical anthropologist who has performed large-scale studies on skeletons from the Eastern Mediterranean, stated that the Greeks may have paid a price. Phytic acid inhibits intestinal iron absorption and may cause iron deficiency anemia. At least some of the abnormal bone porosities found in Greek skeletons may be attributed to the barley diet (Angel, cited in Cohen & Armelagos, 1984).

With respect to historical events, we know that in mid-3rd millennium B.C., the irrigation systems of Mesopotamia began to have heavy concentrations of salt. Extensive studies were conducted by Robert McC. Adams, now in charge of the Smithsonian Institution. He surveyed the ancient irrigation ditches, and with cuneiformists explored the economic records of the available clay tablets. Yields were given in volume, but we are unsure of the conversion; yields before the problem appeared seem too high. The ratios, however, indicate a drastic reduction in both wheat yield and area planted. By the end of the 3rd millennium, Mesopotamia had converted to a near monoculture of barley. Wheat was hardly grown at all. The interpretation is that salting problems forced this change in food crops, since barley is much more salt tolerant than wheat. Still, the records indicate that even before the dramatic shift, barley was the more important crop (Adams, 1965).

But the latter part of the 3rd millennium B.C. was even more of a disaster for Egypt. The Old Kingdom was the glory of the world; there was no civilization on earth to match it. It built the pyramids and was the granary of the world. The people lived well and the arts flourished. It was opulent compared to other civilizations of the time. But at the end of the VIth Dynasty, the Old Kingdom collapsed and Egypt went into eclipse. This was the First Intermediate Period at about 2160 B.C.

No major buildings were constructed for about 170 years; we do not even have a complete list of the kings of the period. The small amounts of literature from those years that did come down to us are stark and eloquent. Some of the phrases that survived include:

'Everyone is dying of hunger on this sand-bank of hell.' 'All of Upper Egypt was dying of hunger to such a degree that everyone had come to eating his own children.' 'Plague stalks through the land and blood is everywhere . . . the towns are destroyed and Upper Egypt is become empty. . . . The crocodiles are glutted with

what they have carried off. Men go to them of their own accord. . . . Men are few. He that lays his brother in the ground is everywhere. . . . The storehouse is bare, and he that kept it lies stretched out on the ground. . . .' (Bell, 1971; Erman, 1927)

What happened? How could the granary of the world suffer devastating famine? It seems that the Nile had failed. A series, perhaps a long series, of low floods on the Nile resulted in crop failures. The glorious Old Kingdom fell into eclipse. An American equivalent would be if no snow came to the Sierra Nevada and the Cascades for several years in succession. Suppose it did not snow in the Sierras for six years? Who would be left in California? This kind of disaster is hard to imagine, but IT CAN HAPPEN! It has happened; history tells us so.

Was this the only event of its kind in history? By no means. In Ancient Egypt, it happened again. After the First Intermediate Period, the Middle Kingdom arose and flourished brilliantly. It, too, collapsed in the Second Intermediate Period ca. 1200 B.C. The cause seemed to be the same. History tells us these things can happen. They do happen.

For several years, I worked with a group of Biblical scholars in Jordan near the Dead Sea. Our target was several Early Bronze (EB) sites which were part of a large example of EB sites throughout the Near East. The general picture was that EB-I left few traces and few bronze artifacts. In EB-II, small towns or large villages appeared and defensive structures were sometimes built. EB-III flourished throughout the region. Towns were walled for defense. At the close of EB-III, the towns were destroyed and, although the reasons are obscure, layers of ash reveal some kind of conflagration. At Numeira, a toppled tower crushed two people, suggesting an earthquake. Whatever the ultimate causes, the Egyptian Intermediate Period had echoes throughout the Near East.

The EB-IV people who followed did not live in towns; they were tent people. What we know of them comes mostly from cemeteries, because they buried their dead in the same necropoli as the earlier EB people. The evidence seems to illustrate the traditional contest between the desert and the sown. Sometimes the farmers win; sometimes the desert wins. The site of Numeira has some phonetic similarity to the biblical Gomorrah. The language of its destruction closely parallels the Egyptian descriptions: "The whole land will be a burning waste of salt and sulfur — nothing planted, nothing sprouting, no vegetation growing on it."

Other evidence includes salt tongues that formed in the Dead Sea and other salt lakes. Lake Maribad dried up and vegetation on the bottom burned. From as far away as France, timber trees died of drouth (Crown, 1972). Abandonment of sites and cessation of rock paintings provide evidence of people moving from the Sahara (Butzer, 1976). Hordes of nomadic tribesmen, forced from their desiccating steppes, invaded settled agricultural lands. The Akkadian Empire fell apart 2230-2130 B.C. Ebla was sacked and burned 2250 B.C., and Troy was destroyed 2149 \pm 97 B.C. The number of agricultural communities in Turkmenistan declined, reaching a low point about 2100 B.C. (Masson, 1968). Towns, cities, and villages, including Jericho, Numeira, Bab edh-Dra'a, Bethshan, Khirbet Karak, and Ai, were sacked and burned (de Vaux, 1971).

Disasters due to factors other than drouth may strike. Local famines were common in Europe throughout the Middle Ages, but the decades of 1290-1300 and 1310-1320 were devastating throughout most of Europe. The causes were complex: some were sociopolitical (rapacious landlords and impoverished peasants), and some were demographic (too many people). Life and society were precarious and vulnerable, but the crop failures basically resulted from too much rain. Land was too wet to work; planted crops rotted in the field. Diseases ravaged both crops and the human population. In some localized regions, over 50% of the people died in a decade. The total populations of Europe may have been reduced by one-third. All of this was a prelude to the Black Death that raged through Europe 1347-1350. This leveler reduced the population sufficiently that famine became less of a threat; there were far fewer mouths to feed (Gottfried, 1985).

I am not forecasting gloom and doom, but merely pointing out some lessons from history. Disasters on a continental scale have happened, and we must consider the extreme vulnerability of the world today. We now have enormous urban populations all over the world that are entirely sustained by a relative handful of farmers, and these in turn are completely dependent on the whims of weather and climate. No system of reserve food storage could possibly outlast a few years of widespread crop failures. These things can happen; history tells us so.

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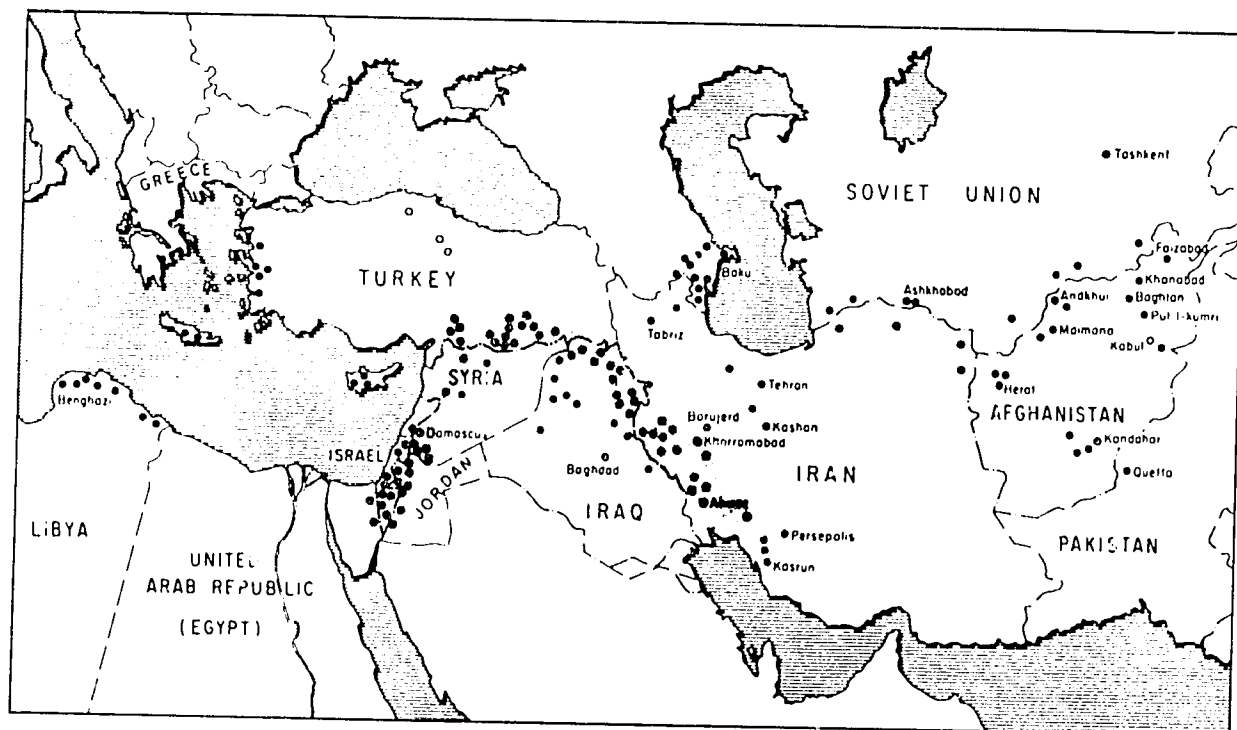


FIGURE 1. Known locations of wild or weed barley. In the shaded region, populations may occur in fairly primary habitats and may be truly wild. Populations are also known in Morocco and Tibet.

Methods Used in Transferring Technology from the Laboratory to the Producer: Economic Considerations

G. Edward Schuh*

There is a growing consensus among agricultural development specialists and policy makers that the making and diffusion of new production technology is the key to agricultural development and an important source of new income streams for the population. (See Hayami & Ruttan for the state-of-the-art on this perspective.) Moreover, organized research is now generally recognized as an efficient way to produce this new technology. In organized research, the social rate of return to investments is quite high. The empirical evidence supporting this perspective is almost unchallengeable, with estimates of rates of return ranging from 25 to 35% at the low end to over 100% at the high end (Hayami & Ruttan).

In contrast, less agreement exists on the need for organized, public sector systems to transfer this new technology from the laboratory and research station to the producer, or on what means to use in bringing about the transfer. Traditionally, in many developing countries, the extension services preceded the establishment of organized research systems, the assumption being that an ample supply of new technology is available but some means is needed to motivate and teach producers. At the other extreme, it is often argued that formal or organized systems for transferring the new production technology are not needed because farmers will adopt it once it becomes available, or the private sector will organize the transfer mechanisms.

Even when the need for some formal or organized system of technology transfer is recognized, much disagreement exists over the best means to do it. Proponents of alternative systems, such as television and the American extension system, are articulate and vociferous. The debate continues even as investments are made in the capacity to produce the new technology.

Because of this ongoing debate, I have chosen to divide my remarks into two parts. In the first part, I will discuss some of the economics of technology transfer in terms of the systems at large. This might best be described as the macroeconomics of

technology transfer. Then, in the second part, I will discuss the economics of the adoption of new production technology at the producer level — the microeconomics of technology transfer.

In both parts, it is worth keeping in mind that in the case of agricultural modernization and development, we are primarily considering *process* technology. Process technology consists of innovations which, if adopted, will lower the cost of production. Product technology, which consists of the introduction of new products, is less common in agricultural development, although not unimportant.

The Economics of Technology Transfer Systems

Process technology comes in a variety of forms. An important part is imbedded either in new inputs or in improvements to the quality of inputs already used. Examples of the former include the introduction of modern commercial fertilizers, pesticides, and modern instruments and equipment. Examples of the latter include improvements in the quality of seeds, of machinery and equipment, and of breeding stock.

Process technology also includes knowledge or information about new ways of doing things, such as changes in plant spacing, alternative ways of using fertilizers and pesticides, and new animal husbandry systems. In this case, technology transfer has to do with the diffusion of new information or new knowledge.

The economics of information diffusion is different from the economics of distribution and adoption of new or improved inputs. Considerable debate still exists about the appropriate systems to transfer the technology since there is often disagreement about the essence of the process. Part of the debate arises because the economics of the various systems change with the level of development of the country

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or region in which technology transfer is desired. Analysts from regions in different stages of development tend to have varying perspectives on what is important.

Several factors important to the economics of alternative technology transfer systems vary from one developmental stage to another. The first is the real wage, which influences the cost to society of agents for the system. Another is the level of general education in the society, which influences the supply of cognitive skills available to understand the new technology. Still another is the state of development of the educational system to produce the agents for the system. And still another is the state of development of the mass media.

We will now consider specific systems of technology transfer. A traditional system in much of Latin America (and one that is still all too common in that region as well as in other parts of the world) is known as *fomento*. This system takes a variety of forms, but it usually involves making available the services of some modern input or the inputs themselves from the public sector, either at no cost or at less than true economic cost. An example is providing the services of improved breeding stock to producers for improving the quality of their herds. Another is making available the services of large tractors and equipment to lower production costs.

The economics of *fomento*, either private or public, are usually quite bad — except for the few who can benefit from such a system. Budget limitations can severely limit the availability of such services. Therefore, several non-price rationing systems are used to equitably distribute available services. Nepotism and corruption surface quickly when such inputs are made available on a subsidized basis, and those least needy of public subsidies are usually the principal beneficiaries of the system. The goal of such systems is to promote the use of higher quality inputs. However, this is usually done only on a limited scale. This system is now generally discredited, although examples still remain.

The *fomento* system illustrates an important dimension of any technology transfer system, i.e., the need to have a system whereby modern inputs are made available to producers. Markets are often the best means of providing inputs to producers. But markets don't just happen. The inputs must be produced or imported and a distribution system developed.

Another generally discredited system is the use of demonstration farms where modern techniques are

used on an entire farm and thus the common producer can see how the new technology is used and how it performs in a complete farm operation. The high cost of this system limits its impact. Moreover, such systems lack credibility since producers perceive that public sector farms benefit from subsidies they don't have. Equally as important, the performance of these farms suffers since they tend to be operated by people who are not true entrepreneurs.

Demonstration *plots* are another matter, however. They are often an effective element of a more general system of technology transfer, and they enable the transfer agent to demonstrate to the uninformed just what the new technology can do and how it operates.

A popular technology system in many parts of the world today, and one promoted by some parts of the World Bank, is the T&V system. This system involves a cadre of agents working intensively with producers in a technical assistance mode. The typical system has one agent for each 10 to 20 producers. An intensive system of monitoring and verification is built into this system in order to verify whether the agents are doing their jobs and whether the recommendations are valid.

The T&V system is effective in *reforming* a moribund extension service. It forces the agents to interact with the producer, and provides a means of upgrading the agents' skills and knowledge. As a general system, however, the economics are again bad. The size of the extension service would have to be quite large in order to reach all producers. Even though salaries are low in developing countries, budget resources are limited.

The use of technical assistance with individual producers is a more general issue, and one that goes beyond the T&V system. The program of the U.S. Extension Service was predicated on extensive use of individual technical assistance, with the agent working directly with the producer, teaching new techniques and solving specific problems. This approach is effective at certain stages of development and with certain groups of producers, especially if the agent plays a true educational role. Working directly with producers gives the agent an important feedback mechanism to identify problems at the farm level. But for an economy that is at the stage of development of the United States, the main value of the technical assistance approach is in this feedback role. This role can be fulfilled by using the approach on a fairly modest scale.

When a society reaches a high stage of development, with widespread literacy and the availability of mass media, the farm-level technology transfer system essentially becomes a part of the research system. Its value is in providing a link between the producer and the researcher so the latter can know what problems the producer is experiencing, and can determine how new technical innovations are working at the farm level. The producer obtains new knowledge and information more efficiently, in a social sense, from the mass media or from private-sector technical assistance services. In this context, extension services should focus their efforts on adult education programs which teach principles in classroom settings under conditions which recognize the opportunity costs of the producers.

This raises another important economic issue. At some stages of economic development, extension services substitute for the general education system. They are necessary because the producers lack the literacy skills to take advantage of written material. As the level of literacy rises in a society, the technology transfer function will decline in importance for the public. This does not mean that it should disappear, but it does mean the extension service's goals should change as economic development proceeds, shifting from an emphasis on technical assistance to an emphasis on adult education and public affairs.

In this context, we must recognize an important complementarity between the diffusion of new production technology and education. The demand for education rises as new technology is diffused into the economy, because cognitive skills are needed for decoding the new knowledge. In fact, the rate of return to investments in education tends to rise as the rate of diffusion of new technology increases. Widespread prevalence of general education increases the rate of return to investments in agricultural research since the speed of adoption will influence the payoff from agricultural research.

To conclude this section, there is no single answer concerning what is the best or most effective means of technology transfer for agriculture. It depends on the stage of development of the economy or region, and the particular institutional challenges faced by the sector. More attention should be given in designing individual systems to the economics of the alternative systems and of the process itself. An important part of the system's economics depends on the character of the technology. Individual technologies vary in the complexity and in their cost to the producer.

Some Microeconomics of Technology Transfer

An important issue in the transfer of new production technology is whether it is profitable at the producer level. This is especially important in adopting new or higher quality inputs. But it is also important in adopting new techniques of production, and the economics of information acquisition is also important at the producer level.

New or improved inputs will not be adopted if they are unprofitable to the individual producer, so it is not sufficient to have a new technology which increases output or yields. The increase in output must be worth more than the production cost or the technology will not be adopted. Many extension services and extension agents have been discredited because they failed to recognize this important point.

There are a number of complicating factors in this issue. The first is the complementarity between or among the various components of the production system. For example, an important feature of the improvement in the quality of hybrid corn seed is its higher response to the application of commercial fertilizers. Thus, its payoff comes by using improved seed in combination with the application of fertilizer. If fertilizer is so costly that it is unprofitable to use, even with the improved variety, little will be gained by using the seed alone. Promoting the adoption of hybrid seeds under these conditions only discredits those who do so. Producers quickly figure out the profitability of the new technology.

This issue has more general dimensions. For example, improved varieties may require the use of fertilizer, water, and pesticides if they are to be profitable. This is what gave rise to the tendency to advocate *packages* of recommended practices as the means to obtain more widespread adoption of any individual technology.

Another complicating factor is the opportunity cost of the time of the producer, a factor which has not received the attention it deserves. New technology or technological packages differ in their labor intensity. If the opportunity costs of the producer's time are high, technologies that are more labor-intensive probably will not be adopted.

Two examples illustrate the point. The first is from Plan Puebla, the intensive technology program for small producers of maize in Mexico. In the 1970s, when the Ford and Rockefeller Foundations and others were extolling the success of this project, I was more impressed by the limited number of producers who adopted this package, especially in light

of its intense promotion. Knowing something about the region, I hypothesized that the problem was the high opportunity cost of the producer's time. The recommended package was labor-intensive because it increased labor requirements, and off-farm work in the region was widespread.

Manuel Villa Issa, a Mexican student of mine at the time, addressed this issue in his Ph.D. dissertation. He found a near-perfect correlation between the failure to adopt the technology and participation in off-farm work activities. Those who adopted the technology tended not to work off the farm. The opportunity costs of their time were low and they adopted the labor-intensive technology. An interesting side feature of Villa Issa's research was that the net family income of the two groups of producers (adopters and non-adopters) was not significantly different. They just earned it in different ways. This says something about the "quality" of the human agents in the two groups.

The second example is from Kenya. A T&V project in that country promoted the intercropping of maize and beans in narrowly spaced rows. The recommended technology obviously increased production compared to traditional techniques, but it was a labor-intensive system.

The producers were not receptive to the recommended package. A few questions soon uncovered why. Labor was scarce and expensive in the region, so the producers utilized family labor instead of hiring additional labor. This was not a case solely of the opportunity costs of family labor, although it may have played an important role. It does point out that assuming unlimited supplies of labor under developing-country conditions is not always warranted.

Input substitution issues are also important in considering the economics of adopting new production technology. It isn't just the price of the product relative to the price of the new or improved input that matters. The price of land has a great deal to do with the adoption of commercial fertilizers since fertilizer is an important substitute for land. Rising land prices lead to widespread adoption of fertilizer. Similarly, herbicides and mechanization are substitutes for

labor. As labor prices rise with economic development, the tendency is to make more use of labor substitutes.

Risk is another factor in determining whether producers adopt a new technology. New innovations involve technological risk and producers may discount the expected increase in yields, especially if they are barely subsisting and budget constraints are severe. One means to promote the new technology is to find ways of transferring some of this risk to other parts of society. Alternatively, increasing price stability may induce producers to bear more technological risk.

Finally, increasing economic literacy is a way to make the adoption of new production technology more socially efficient. Increased knowledge of the economics of the adoption process, and of the future economic outlook, will help the producer in adopting the new technology only under economically rational conditions.

Concluding Comments

Technology transfer involves a great deal more than the production of new technology or technological packages. The design of the system to diffuse the new technology has important economic dimensions. Similarly, the adoption of the technology at the level of the producer also has important economic dimensions. Failure to consider the economics of the design of the system or of the adoption of the technology by the producer can lead to a lot of frustration, the failure to realize the benefits from investing in the production of the technology, and inefficient development policy. The economic dimensions of both sets of issues need to be kept high on our agenda.

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Transferring and Understanding New Technology: Sociological Implications

Keith Jamtgaard*

One of the more interesting situations we can observe today is that of farmers in parts of Eastern Europe. They are in a quandary, and a better understanding of their predicament helps illustrate one of the points I would like to make concerning sociological implications of agricultural technology.

London's *The Economist* ("No Yeomen They," 1990) reports that Eastern European farmers are resisting the notion that they should be given ownership of the land now held in state farms and coops. Why? We in the West are sometimes guilty of simplifying the events in Eastern Europe because they embrace capitalism; by so doing, however, we can easily overlook some of the more sociologically interesting questions being revealed by large-scale social changes now underway.

Why should the members of cooperatives not be interested in becoming independent farmers? *The Economist* suggests that they have heard the stories passed down from an earlier generation (or those old enough recall for themselves) concerning the experience of farming 15 acres, divided into a dozen strips, oxen-powered plows, and the tremendous risks and limited rewards that were associated with independent farming. Although the level of technology and the farm sizes may not be the same, the great risks and scarce rewards of agriculture in modern capitalism are very real indeed.

Whatever else they did not do, the collective farms did address some important needs of agricultural populations. While they probably did not intentionally enrich hard-working coop members, they did reduce the risk of farming, they provided a secure job for life, and they maintained a stable agricultural population in rural areas. For all of the advances in productivity associated with advanced capitalist farming, these legitimate concerns of rural agricultural populations have not been adequately addressed. It is not the purpose of this paper to mount a defense of the agrarian enterprises produced by the socialist governments of Eastern Europe.¹ However, it is helpful to consider the plight of the Eastern European farmer as we sort through some of the questions raised by technology transfer.

Agricultural Technology and Social Change

The goal of this paper is to discuss, from a sociological perspective, what our intentions should be in the development and transfer of agricultural technology for producers in semi-arid areas, and where this fits into the larger picture of the kinds of changes these rural populations desire. Perhaps a more relevant formulation of this question is: What kinds of change should we strive to achieve using our skills at developing agricultural technology, and on whom should we focus our efforts?

First of all, it is clear that there are different levels of social change. One is macro-level structural change. The major shifts taking place in Eastern Europe are examples of this. They are characterized by a major change in the role of the state, the creation of a new social class, the destruction of an existing class, or changes in the distribution of power among social classes.

Except in rare circumstances, like that of Eastern Europe, most of us do not work in anticipation of achieving results at this level. However desirable we may view the need for fundamental change in social structure, we usually assume these changes will occur independently of our actions. There are exceptions to this, however, and some sociologists have documented instances in which the introduction of new agricultural technology in the Third World has had the effect of weakening the situation of the poorest social classes (Pearse, 1980; Griffin, 1974; Deo & Swanson, 1990). We do therefore need to be aware of the potential impact the introduction of new technologies can have upon the social structure.

Two major sociological implications arise in conjunction with the transfer of agricultural technology. The first concerns what is to be transferred. I argue that this question really reflects the issue of who is involved in the definition of the problem that technology is intended to resolve. The second concern

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probes the issue of who should be the focus of our efforts. I argue that the individual may not be the appropriate unit on which to focus our attention.

Technology Transfer: A Participatory Approach

One of my colleagues summed up the frustration that social scientists often experience with technology transfer by describing it as the process of tinkering with reluctant human "software" to correctly utilize laboratory designed "hardware" (McCorkle, 1989). Technology transfer contains within it the notion that farmers must somehow be persuaded to adopt technologies which are in their interest. The problem here is that farmer interests are being defined by policy makers, or academicians far removed from the farm gate.

A substantially different approach is presented by an emerging paradigm known as "participatory research" (Chambers, 1983; Richards, 1985; Fernandez & Salvatierra, 1989). In this approach, the problem definition, as well as much of the actual research, is conducted by producers themselves. Scientists do have a vital role, but they participate in the capacity of consultants to participating producers rather than as principal investigators. The advantage here is that local interest in social change is maximized, and the prospects for self-reliant development are improved over an effort engineered from the "outside."

Elements of this paradigm have already gained recognition, particularly the notion of on-farm research. However, potentially serious social barriers remain to be overcome before this approach will see greater use. In a sense, these issues all stem from the perception that knowledge generated, at least in part, in the field by farmers (rural people's knowledge) is of lesser social value than the same knowledge developed in the laboratory by scientists (scientific knowledge). The functioning of this prejudice, particularly among extensionists and scientists, has been noted for some time (Chambers, 1983). I will add that there sometimes exists a significant degree of prejudice about rural people's knowledge among rural people themselves.

Scientific knowledge, which has been developed by a powerful, prestigious, and wealthy organization, tends to confer power, prestige, and often wealth, upon three groups — those who develop, distribute, or use these technologies. Therefore, it is a cause for some concern among these groups when a technology arrives which has been developed with the

extensive participation of individuals who tend to be powerless, of low prestige, and who are poor.

One barrier to participatory research not often discussed is that which exists among producers themselves. Farmers may be reluctant to accept technologies which have been developed by their neighbors, even if those technologies are better adapted to their needs than research station technologies. Lacking the association with wealth, power, and prestige that research station knowledge has, indigenous knowledge begins at a disadvantage in the eyes of some producers. The downgrading of local capabilities is one of the most damaging legacies of colonialism and dependency. Yet one solution is relatively simple. As professionals, we may increasingly question the power, prestige, and (even more likely) the wealth that we control, yet these clearly are of some value as symbols influencing the adoption decisions of farmers. In this sense, these symbols represent a type of social, as well as real, capital over which we exercise some control. To the degree that we can validate rural people's knowledge and problems through our professional talents, we help reduce the negative meaning that "indigenous" has for many people. Another more intuitive scenario sidesteps the role of the professional altogether. If indigenous knowledge is found to be useful, those who adopt it will receive their own rewards, and those who fail to, for whatever reason, will simply be left behind.

Another involved group is the extension sector. Richards (1985) has described an extension strategy that he calls "sideways extension." In this approach, the extension network actually assists in spreading to other farmers the best of the innovations developed by the farming sector (or "informal" sector). Although Richards does not provide evidence, it is not hard to imagine that this kind of activity would be viewed with alarm by extensionists accustomed to a different flow of information, and concerned about the potential loss in prestige this represents for them. Richards suggests one possible strategy. Recalcitrant extension agents could be replaced by successful farmer innovators. Another strategy would be to place greater emphasis on providing more occasions for farmers to exchange information among themselves. Expanded opportunities for field days, farmer organized workshops, and informal networks would also be useful here.

A problem which strikes even closer to home for many of us is that of apprehension over the status of participatory research in the academic and donor

community. As one researcher said, in describing how the scientific community would probably react to research on problems that peasants declared to be of highest priority: "No Nobel prizes have been awarded for work on donkeys, goats or mules" (Chambers, 1983, p. 79). The editors and editorial policies of academic journals influence what is published, and therefore shape the academic reward structure for those who do engage in participatory research with farmers. The study of rural people's knowledge is unlikely to rank high on the list of priorities of the editor of "hard" scientific journals, which are distinguished by their rigorous standards (Chambers, 1983). Fortunately, there are a growing number of journals (usually having a title beginning with "Ethno") which actively seek these kinds of articles.

These admonitions are not intended to frighten anyone away from doing participatory research. In fact, I feel that it represents the best hope for agricultural technology in contributing to rural social change. This is another illustration of the degree to which the development of agricultural technology is a social process. The issues listed above simply represent some of the next hurdles to be overcome.

Individual Interest and Community Impact

The other question I would like to examine is: What is the appropriate social unit upon which to focus our efforts? Most activities of sociologists participating with agricultural development efforts are directed at achieving change at the level of the individual (producer). This is not to say that macro-level issues, such as cultural, institutional, or policy factors are unimportant — only that we usually assume our time and efforts are best invested in understanding and improving the situation of individuals.² As a program of action, we are confident that if we can improve the situation for an important segment of individuals, this has major and beneficial consequences for the larger social system.

One of the principal means for achieving social change in the rural areas of the United States is the diffusion of agricultural technology (Rogers *et al.*, 1988). The knowledge base surrounding the transfer of agricultural technology tends to be directed toward the level of the individual producer and, in particular, on the decision of whether or not to adopt a new agricultural practice. However, focusing exclusively on the individual can have serious consequences for programs interested in achieving social change.

The situation of economics is interesting in this regard. Economics has become the most "scientific" of the social sciences, perhaps partly because it is so developed as to sometimes be the target of criticism from the other social sciences. One criticism sometimes leveled at economic analysis concerns its scope. From the perspective of sociology, much of the power of economics comes at the cost of its limited scope. Neoclassical economic analysis tends to be limited to those who are most directly involved in an action — a decision to adopt an agricultural technology, for example. Usually left out of economic analyses are those who are not parties to an action, but who are nevertheless affected by the action. The point here is that an action which maximizes your utility function may have profound and negative consequences for my utility function (Coleman, 1987).

One of my favorite illustrations of this point, and one which I believe is highly relevant for semi-arid agriculture, is the illustration of the tragedy of the commons. Many livestock producing regions of the world have pastureland which is held under common property tenure. Garret Hardin (1968) argues that an individual livestock producer will find it to be in his or her individual interest to add additional animals to the commons, since the benefits of doing so will accrue to that individual, while the costs (in decreased forage) will be borne by the other members of the commons.

This kind of logic has been found to operate in the western United States, where livestock operators were accused of severely overgrazing the public rangeland (Foss, 1960).³ However, the record is less clear for traditional societies, a number of which have apparently used common property for centuries (Gilles & Jamtgaard, 1981). Runge (1981) points out that the profit maximization calculation for each individual actor is affected by the decisions of others who also have rights to common resources. A simple individual calculation of utility no longer models the decision making process of producers using a common property resource. The problem to be overcome in these situations is that of uncertainty. Given assurances of the conservation-minded intentions of others, the strategy for the individual becomes one of curtailing behavior damaging to the common good as well.

In addressing the wider implications of this notion, Coleman (1987) notes that social norms and laws have the effect of entering the utility function of individuals to constrain the individual from taking actions which would have negative consequences for

others. In other words, social norms represent a claim by some wider group of people to control the actions of individuals, even when following the norm produces an outcome which represents something less than would be the case if the individual's self-interested actions were taken.

Relevance for Barley Producers in Semi-Arid Regions?

Cultivated land is usually considered to be under the control of individuals. However, at the margins of agriculture, control is often times something less than the unrestricted right to use and dispose of land that we interpret as private control. This is particularly the case in semi-arid and mountain areas where peasants use extensive agricultural technologies. Fallowing is a key regenerative feature of farming in marginal areas, and during the fallow stage, land is often subject to rights by other members of the locality.

Guillet (1981), in discussing the case of cereal and tuber producing regions of the Central Andes, points out that community rules govern activities during the cultivation stage. Rules regarding planting, harvesting, and crop rotation are essential features of peasant agriculture in areas where specialization and intensification are difficult. These agricultural systems are referred to as "sectoral fallowing systems."⁴ Land is divided into a number of sectors, and households have access to plots within each of the sectors. The length of time that sectors are cultivated varies, but the length of the fallow period exceeds the period that a sector is cultivated. Each plot within a sector is sown to the same crop according to an agreed upon rotation-fallow cycle. Households have rights to cultivate plots within each of the sectors, but they are constrained by community rules governing the size and number of plots that they may have, the crops that will be grown in the fields, and the timing of planting and harvesting. Rights to cultivate plots are not permanent. Periodically there are land redistributions which bring use rights into closer alignment with need. During the period when a sector is fallow, other households have grazing rights to the land that was previously held by a household, and so land is also subject to usage rights which go beyond the individual household.⁵ As the possibilities for agricultural intensification increase, as in the case of irrigated land, the usefulness of communal controls declines, and private control is more likely to be found (Guillet, 1981).

Netting (1976) argues that there are several types of land use exhibiting advantages for communal

rather than individual rights over land: (1) If the value of the production per unit area is low, (2) if the frequency and dependability of use or yield are low, (3) if the possibilities for intensification or improvement are few, (4) if the size of land surface required for effective use is high, or (5) if the resource cannot be effectively exploited by the labor and financial resources of a single household. Semi-arid regions where extensive farming techniques predominate meet many of these conditions. Some communal participation in dryland farming is therefore likely. From the perspective of an individual, these represent significant externalities which serve to severely constrain their utility functions. From a community perspective, however, these rules offer a guaranteed minimum livelihood, and assurances that there will be opportunities to engage in vital strategies such as labor exchanges. An individual who adopts a new crop, or violates rules regarding the rest-rotation cycle, poses a threat to those who have fewer resources, and who depend upon devices such as labor exchanges for survival; for this reason, innovators are often severely sanctioned by the community.

This is not to say that change is impossible. Historical studies of peasant communities in other regions of the world have demonstrated that communities will adopt new agricultural technologies over time (Vincze, 1980). The incorporation of a new crop into the rotation cycle, or discarding the fallow cycle in favor of a legume crop, are changes that sectoral fallowing systems often undergo. These changes tend to loosen the degree of communal control over household production, expanding the degree of individual control over production. The key to understanding change is that it is necessary to readjust the unit under consideration from that of the individual to the community. Change takes place as communities of people collectively decide to relinquish certain rights they have placed upon the use of resources. Sometimes old communal rights are replaced with rights by new collective bodies.

Bourdieu (1958) describes the traditional agriculture of Arabic-speaking peoples. These bring to mind similarities with peasant agriculture elsewhere. There were once systems of sectoral fallowing with annual redistributions. However, due to a number of causes, these annual redistributions have tended to be replaced by permanent rights to cultivate the same plots. Certain rights are still held by a larger unit than the individual — the extended family. Individuals have well-defined rights to farm property held in joint possession by the extended family. In such

cases, usage rights are more advantageous than strict property rights for both individuals and extended families. They provide a secure livelihood for those individuals who would not be able to survive on the scattered tiny plots to which they would be legally entitled should property be distributed by a court.⁶ From the perspective of the community, joint possession provides a measure of protection from the wastefulness of individuals, as well as from the uncertainties of environment.

Just as for the members of Eastern Europe's struggling collective farms, for peasant farmers in semi-arid or mountain areas of the Third World, achieving change requires first understanding the needs addressed by existing production and social systems, as well as the social norms which exist concerning production. The next step is to work with groups of farmers to achieve a consensus which addresses collective concerns regarding proposed changes. As one well-known sociologist pointed out: "Much of what is ordinarily described as nonrational or irrational is merely so because the observers have not discovered the point of view of the actor, from which the action *is* rational" (Coleman, 1990, p. 18).

Endnotes

¹It would also be incorrect to suggest that all Eastern European farmers face this difficulty. Poland never experienced the radical reform witnessed in neighboring countries. *The Economist* ("No Yeomen They," 1990, p. 16) also points out that farmers in the Bihor district of central Romania are vigorously pursuing privatization of their operations.

²Even if our goal is to achieve policy changes within a society, we must at some point deal with individuals who create and implement policy.

³A useful distinction should be made between "common property" and "open access" (Runge, 1981). Open access, where overuse can be expected, is conceptually distinct from a commons. Where a specific group of users can be identified, a structure of usage rights tends to emerge. This is "common property." Where there is no defined group of users, and usage rights do not exist, the property may be described as "open access." Calef (1960) argues that in the case of the Western public rangelands, there was a structure of usage rights among the rangers. The problem was one of steady encroachment of homesteaders upon the best lands, and the uncertainty that this produced for ranchers who depended upon these lands for grazing.

⁴See Orlove and Godoy (1986) for a discussion of these systems for the Central Andes.

⁵Debate even occurs as to whether the stubble from cereals is subject to the rights of the individual as cultivators or the rights of the larger community as pasturage (Jamtgaard, 1984).

⁶Bourdieu (1958, p. 74) says that examples exist of beneficiaries of inheritances being awarded "two or three square centimeters from one hectare held by several hundred joint owners."

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Global Status of Barley and Its Constraints

D. H. B. Sparrow*

Global Status of Barley: Area and Production

Barley has the widest geographical range of any crop plant. It is grown on the Equator in Kenya and Ecuador, within the Arctic Circle in Scandinavia and Alaska, below sea level on the Dutch polders, and high in the Andes.

In area and production, barley ranks fourth among the cereals after wheat, rice, and maize. Although its production is only one-third that of wheat, its average yield on a world basis is comparable (*Table 1*). This is surprising because wheat is more likely to be the favoured crop being grown on the better soils with better fertilizer inputs. Wheat is also more likely to be irrigated than barley where water is available. Over the last 30 years the relative proportions of wheat and barley have not changed greatly, although there was a slight increase in barley during the 1970's (*Table 2*).

On a regional basis, the greatest area and production of barley is in the USSR, with 38% and 29% respectively. Europe as a whole comes second in area (24%), but with a greater production (40%) due to the very high yields now being achieved in north-western Europe (*Tables 3 and 4*).

Average yields by the regions, as depicted in *Table 3*, tell an interesting story and may illustrate possible future improvements in productivity. For example, the very low yields for North Africa include those from Egypt that are well above the average for the region since some of the crop is irrigated. In contrast, the Australian figure is about half a tonne per hectare higher from closely similar climatic conditions. The same comment could also apply to several of the semi-arid countries in Asia, where the average yields range from about 0.7 tonne/hectare to a little over 2 tonnes/hectare, approaching the level of southern Europe, which is marginally semi-arid and probably more intensively farmed. The yield levels in the southern three countries of South America are surprising given the excellent rainfall conditions of Uruguay and parts of Argentina.

A rough calculation suggests that about a quarter of the world barley area is grown under semi-arid conditions to produce about 20% of the world crop.

A very high proportion of the world barley crop is used in the country of origin. From figures available (*Table 5*), only about 10% of the crop enters the export market. This contrasts with wheat where the figure is about 18%. The largest importer of barley is Saudi Arabia, followed by the Soviet Union and Eastern Europe; in addition, there are many smaller importers. The European Community is the largest exporter, boosted no doubt by subsidization; Canada and Australia follow. Together with the United States, these four account for more than 90% of the total exports.

Constraints to Barley Production in Semi-Arid Environments

In considering constraints to barley production in semi-arid environments, there are five categories of factors which merit discussion: (1) climate, (2) cropping patterns, (3) soil nutrient status, (4) pests and diseases, and (5) crop utilization. These are not discrete categories nor are they in a particular order, except for the first, since all interact and influence each other.

Climate

Semi-arid climates are notorious for the unreliability of the seasonal rainfall. The moisture available for crop growth can vary considerably at different stages of the crop's development depending on the amount and distribution of rainfall (*Figure 1*). Temperature and relative humidity affect the evapotranspiration load such that in extreme conditions the crop may wilt although soil moisture is adequate.

In winter rainfall areas, described as a Mediterranean climate, a peak of midwinter rain can cause waterlogging on some soil types, with a restricted or

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delayed development of the crop. Winter temperatures can also be low enough to restrict crop growth, as, for example, in Syria, although elsewhere growth may continue throughout the winter, as in southern Australia. In the same areas, a late onset of winter rains reduces the period of crop growth, while an early cut-off of seasonal rains (spring drought) can restrict grain fill and thus yield. Even where moisture is not limiting, short bursts of hot weather during grain filling can disrupt starch synthesis and thus final grain size. Compared to wheat, barley can often escape the worst of a spring drought by reason of its relative earliness, but if too early, in some areas it can be at risk of frost damage to the developing grains. Cultivars and agronomic practices must be tailored to fit anthesis to the least hazardous period of the spring.

There is obviously a wide range of semi-arid environments depending on the length of the rainfall period as well as its reliability. Even the more benign winter rainfall areas of Mediterranean Europe can suffer drought; conversely, drought-prone areas of southern Australia can experience above-average rainfall and a bumper season. The vagaries of the season in these areas present the greatest challenge to breeding for wide adaptability.

Although emphasis has been on winter rainfall climates, it is appropriate to mention another type of climate which could be characterised as semi-arid. Barley and, of course, wheat are grown over winter in areas of summer rainfall where the soil retains sufficient moisture for crop growth during a dry winter. India and Central Queensland fall into this category. In these areas, where water is available, irrigation can be practised — as in northern Mexico and the southwestern USA. In some such areas, the onset of summer rains can provide a major hazard to harvesting, and again manipulation of crop maturity becomes important.

Cropping Pattern

In semi-arid environments, possibilities for ring-fencing the changes in crop species are limited, especially if irrigation is not available. Winter cereals, grain legumes, grass, and legume pastures are traditional to Mediterranean agriculture. In drier locations, wheat:fallow rotations have been used to preserve soil moisture and accumulate nitrate between the cropping phase. Productivity can be sustained in this way, but only at a relatively low level and with some degradation of soil structure. If the fallow can be replaced by a legume pasture containing *Medicago* or

Trifolium species, the results will be greater productivity, including animal grazing, and a better soil fertility and structure. A barley:medic pasture rotation was widely used on the higher alkaline soils of southern Australia during the 1950's and 60's; however, it has declined due to reduction in medic growth from attacks of *Sitona* weevil and other pests and by the economic necessity of closer cropping together with variable fortunes of the wool market.

A grain legume crop, field peas, faba beans, or lupins, in place of the pasture phase, gives good returns to the farmer, but less of the fixed nitrogen is returned to the soil. However, these crops, with their deeper (tap) rooting systems than cereals, do open up the lower layers of soil to improve its structure at depth; they may also extract nutrients unavailable to cereal roots. Experience in Australia shows that wheat and barley go particularly well after faba beans; in the deep, infertile sands of Western Australia, lupins are the preferred crop to interchange with cereals.

So-called double cropping of cereals in semi-arid environments, even barley after wheat, gives a poor return unless nitrogen fertilizer is added. They are really only feasible after several years of pasture but, due to soil nitrogen accumulation, the difficulty is to maintain a good legume stand in the pasture phase for more than one or two years.

Cropping pattern also affects the weed flora present in the crop. Overuse of cereals and/or grass dominated pastures results in the build up of grassy weed species such as wild oats (*Avena fatua*). Although barley, with its early growth and ground covering ability, is an excellent competitor, it can at times be inundated by fast-growing grass species such as ryegrass (*Lolium rigidum*), barley grass (*Hordeum glaucum*), and silver grass (*Vulpia* spp.). When herbicides are not available, a working up of the land after the first rains and a resultant flush of weed seedlings can be an effective control — but timing is all-important.

In the more developed semi-arid areas, herbicides, both pre- and post-emergence, are used extensively to control weeds in all crops. In Australia, for example, the farm bill for herbicides often exceeds that for fertilizers. Overuse of particular herbicides has led eventually to the development of resistant strains of weed species — both grassy and broad-leaved. A disturbing feature of this resistance is that, although it may develop to one chemical, it can sometimes be effective against another unrelated compound. For example, cross resistance to Hoe-grass (diclofopmethyl) and Glean (chlorsulfuron) has

been found in ryegrass which was exposed only to diclofopmethyl.

Nutrient Status

In semi-arid environments the nutrient status of soils is influenced by rainfall in several ways. During dry seasons where legume pasture growth is depressed, nitrogen fixation is reduced, providing less organic nitrogen for subsequent crops. Dahmane (1978) has demonstrated a clear correlation between soil nitrogen level and the rainfall related growth of legumes in previous seasons (*Figure 2*). On the other hand, on sandy soils with poor absorptive capacity, excessive rainfall can leach available nitrogen and phosphate. As a result, midwinter nitrogen starvation is often seen in crops in a Mediterranean environment.

Potassium, magnesium, and calcium are usually adequate in semi-arid regions. Where there is a low level of leaching, an accumulation of calcium carbonate results in a high pH which in turn renders the trace elements manganese, zinc, copper, and iron relatively insoluble and unavailable in sufficient quantity to the crop. Barley is capable of extracting sufficient iron from alkaline soils, and some trace element efficient cultivars have been found capable of a more effective absorption of manganese, zinc, and copper from such soils. This capacity appears to be under simple genetic control, and breeding for trace element efficiency is possible (McCarthy *et al.*, 1988).

The trace element states of soils and of the plants grown in them can have an important bearing on the amount of damage caused by foliar and root diseases (*Tables 6 and 7*).

Toxic levels of boron and sodium can occur where soils have developed from ancient marine sediments (Cartwright *et al.*, 1987). Salt accumulation is a pressing problem in many semi-arid environments; the effects of boron are less well-known, but appear to be quite widespread.

Toxic levels of aluminum and manganese can occur in inherently acid soils, but only in isolated cases in semi-arid environments.

Pests and Diseases

Several of the following papers deal in detail with barley diseases in semi-arid environments. Here it is only appropriate to consider a few ideas and observations on the occurrence of disease in these conditions.

Powdery mildew (*Erysiphe graminis*) and leaf scald (*Rhynchosporium secalis*) are, arguably, the

most important foliar diseases of barley on a world basis. The former is often serious in the early stages of a barley crop, but tends to disappear under semi-arid conditions with warming spring temperatures. The pathogen is highly variable and, as in more temperate climates, resistant barley cultivars are rarely durable. Despite the disappearance of powdery mildew before grain filling, moderate yield losses can occur. This is probably associated with reduced root growth and tillering during early attack. Leaf scald can be more dramatic, persisting to crop maturity; however, because it is spread by rain-splash, seasons of low rainfall or environments where rain is lacking at certain times are usually free of disease. Scald also attacks barley grass, and debris from an infected pasture can become a focus of infection in the following barley crop (Mayfield, 1982).

Less dramatic but equally damaging in semi-arid cereal cropping is a complex of soil-borne diseases. Take-all (*Gaeumannomyces*), bare patch (*Rhizoctonia*), and several root rots (*Bipolaris*, *Fusarium*) are constant but insidious problems. To add further to soil problems, attack by at least two nematode species (*Heterodera avenae* and *Pratylenchus* spp.) can be devastating. The former, a cereal cyst nematode, is widespread, but probably in many cases unrecognised in semi-arid areas. It attacks all winter cereals. While barley is very tolerant, so that frequent cropping can build up the nematode population with little apparent effect on barley, the nematode can be catastrophic on a following wheat crop. Fortunately, good resistance to the nematode is available in barley, in many cultivars and landraces from North Africa — the likely area of the pest's evolution (Sparrow & Dubé, 1981). We have also recently demonstrated resistance in two acquisitions of *Hordeum spontaneum* from Israel. Because the nematode is restricted to a single generation per year, the resistance can be durable for an appreciable time.

Close cropping with cereals as well as the presence of grassy weeds or grass pastures can lead to an increase in soil-borne pathogens. This again points to the importance of mixed cropping and the use of legumes, either for grain or pasture, to break the cycle of infection. Such alternative crops also reduce soil nematodes which hatch from over-summering eggs but fail to find an appropriate host, thus resulting in a reduced population for the next season.

Crop Utilization

The barley crop has several uses and these determine its status in particular areas. None of the

uses are specific to semi-arid areas but, at least in the developing countries, barley is more likely to be used locally or on-farm than exported.

Because of its early vigorous growth, the young barley crop may be grazed by animals, since in winter rainfall areas it can provide the first flush of new growth. If not overgrazed, the crop can still yield a reasonable return of grain. In some areas, barley may be cut green during grain filling, dried, and used as hay; after harvest, the straw, either left with the stubble or baled, can provide further animal feed — rather more palatable than wheat straw but not as nutritious as oats.

Barley grain has been widely used as an animal feed — either as raw grain or as barley meal. The latter can be used directly or mixed with other ingredients and pelleted to form a balanced stock feed. The greatest use of barley is as an animal feed to supply energy in the diet. Until recently, Australia was selling in excess of one million tonnes of barley annually to the Middle East — all for animal feed. Recent local irrigated production in Saudi Arabia and the U.S. export enhancement program have made inroads into that market.

The traditional beverages of beer and whisky account for a smaller but value-added proportion of barley production. The growing of malting barley and the achievement of the specifications stipulated by the malting and brewing industries are confined to particular areas. Barleys from semi-arid regions are suitable for malting and often have a better visual appearance than samples grown in damper climates. Malting barley does provide an important export outlet for Canadian and Australian barley and from some European countries, but is not yet of much importance in North Africa and the Middle East.

Barley's position as a human food has steadily been usurped by wheat. In areas of poor soil where barley grows better than wheat, it may still be a traditional food, or it may be considered a food for the poorer stratas of society. However, recent findings on the ability of diets which include barley to lower plasma cholesterol levels and improve other aspects of human health may bring it back into favour. Both in the USA and Australia, efforts are being made to demonstrate definitive evidence of its efficacy and to develop acceptable foods which incorporate barley into sophisticated diets.

Conclusion

In developing countries, the gap between possible yields and those actually achieved at the farm level is high. The reasons for this are complex, embracing a diverse set of constraints, some of which have been dealt with above. Problems relating to climate and water availability account for about one-third of the gap, and problems relating to pests, diseases, and weeds to another third. Over a period of time, it is the interactions of different technologies that improve crop productivity. Major developments include mineral fertilizers, improved cultivars, and improved crop protection. The interactions of these factors have and will be the chief determinant to boost production in semi-arid regions, as they have been in the climatically more favourable industrialised countries (*FAO Production Year Book*, 1988).

There is a need to raise productivity in ways that do not aggravate fluctuations in production, do not reduce the potential of the environment to sustain production, and that contribute to rural incomes.

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TABLE 1. Comparative area and production of major cereal crops averaged over three years (1986, 1987, 1988).*

CROP	AREA		PRODUCTION		Avg yield (tn/ha)
	Millions of hectares	%	Millions of tonnes	%	
Wheat	223.4	100.0	521.3	100.0	2.33
Rice (paddy)	144.1	64.5	473.5	90.8	3.29
Maize	126.9	56.8	449.5	86.2	3.54
Barley	77.8	34.8	177.5	33.9	2.28

*FAO Crop Production Year Book.

TABLE 2. Production of major cereal crops over 30 years (millions of tonnes; five-year averages).*

YEARS	Wheat	Rice (milled)	%	Maize	%	Barley	%
1961-65	248.6	162.4	85	206.6	83	87.1	35
1966-70	304.6	187.8	62	248.8	82	110.8	36
1971-75	352.2	218.8	62	292.2	83	141.8	40
1976-80	410.0	251.2	61	370.7	90	164.3	40
1981-85	478.6	292.8	61	416.8	87	165.1	34
1986-89	514.0	316.8	62	447.0	87	177.1	34

*FAO Crop Production Year Book.

TABLE 3. World barley area and production by regions averaged over three years (1986, 1987, 1988).*

REGION	AREA Millions of hectares	PRODUCTION Millions of tonnes	Average Yield (tn/ha)
WORLD	77.83	177.50	
AFRICA Northern 5	4.15	4.17	1.01
NORTH AMERICA Canada, U.S.A.	8.65	23.27	2.69
CENTRAL AMERICA Mexico	0.27	0.52	1.92
SOUTH AMERICA Southern 3	0.20	0.34	1.70
ASIA Semi-Arid 13 China/Korea/Japan	10.33 1.78	14.71 4.49	1.42 2.52
EUROPE Southern 4 Remainder	5.10 13.40	12.10 59.10	2.37 4.41
U.S.S.R.	30.21	53.10	1.76
OCEANIA Australia	2.30	3.41	1.48

*FAO Crop Production Year Book.

TABLE 4. Barley area and production by regions as a percentage of world area and production averaged over three years (1986, 1987, 1988).*

REGION	AREA Millions of hectares	PRODUCTION Millions of tonnes
AFRICA Northern 5	5.33	2.35
NORTH AMERICA Canada, U.S.A.	11.11	13.11
CENTRAL AMERICA Mexico	0.35	0.30
SOUTH AMERICA Southern 3	0.26	0.19
ASIA Semi-Arid 13 China/Korea/Japan	13.28 2.29	8.29 2.53
EUROPE Southern 4 Remainder	6.55 17.21	6.82 33.30
U.S.S.R.	38.81	29.91
OCEANIA Australia	2.95	1.92

*FAO Crop Production Year Book.

TABLE 5. World barley trade averaged over three years (1986, 1987, 1988).*

REGION	Millions of tonnes	Percent (%)
IMPORTS:		
EEC (12)	0.20	1.1
Soviet Union	2.70	15.1
Japan	1.30	7.3
Eastern Europe	2.07	11.5
Saudi Arabia	6.97	38.9
		Total: 73.9
WORLD	17.93	
EXPORTS:		
Canada	5.03	28.1
Australia	2.67	14.9
EEC (12)	6.83	38.1
United States	2.13	11.9
		Total: 93.0
WORLD	17.93	

*FAO Crop Production Year Book.

TABLE 6. Effect of rate of zinc supply on severity of crown rot (*Fusarium graminearum*) on six-week-old wheat plants growing in a zinc-deficient sandy soil in pots.*

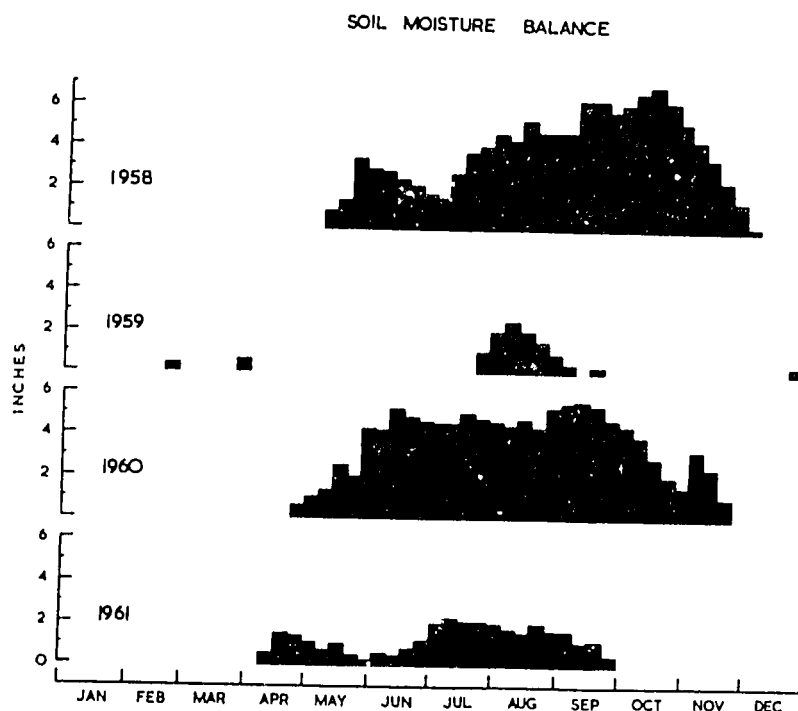
MEASUREMENT	Zn Added (mg/pot)		
	0	0.2	6.0
(i) % of all stem sections infected	47	45	28
(ii) % of upper stem sections infected	66	34	6
(iii) Concentration of zinc in shoots	7.4	8.2	35

*F values for zinc effect are: (i), (ii) 14.4; (iii) 734. Zinc strongly inhibited the upward spread of infection (Sparrow & Graham, 1988).

TABLE 7. Percentage of seminal roots infected by *Rhizoctonia solani* inoculated into a zinc-deficient sandy soil in pots, as affected by zinc fertilizer addition and inoculum density.*

Zn Applied (ug/g)	INOCULUM DENSITY (propagules/kg soil)	
	8	16
0	98	100
12	10	25
LSD* (inoc x Zn)		10

*Thongbai and Graham (1990), personal communication.

**FIGURE 1.** Soil moisture balance over four consecutive seasons, Waite Institute, Adelaide, South Australia. (Finlay & Wilkenson, 1962)

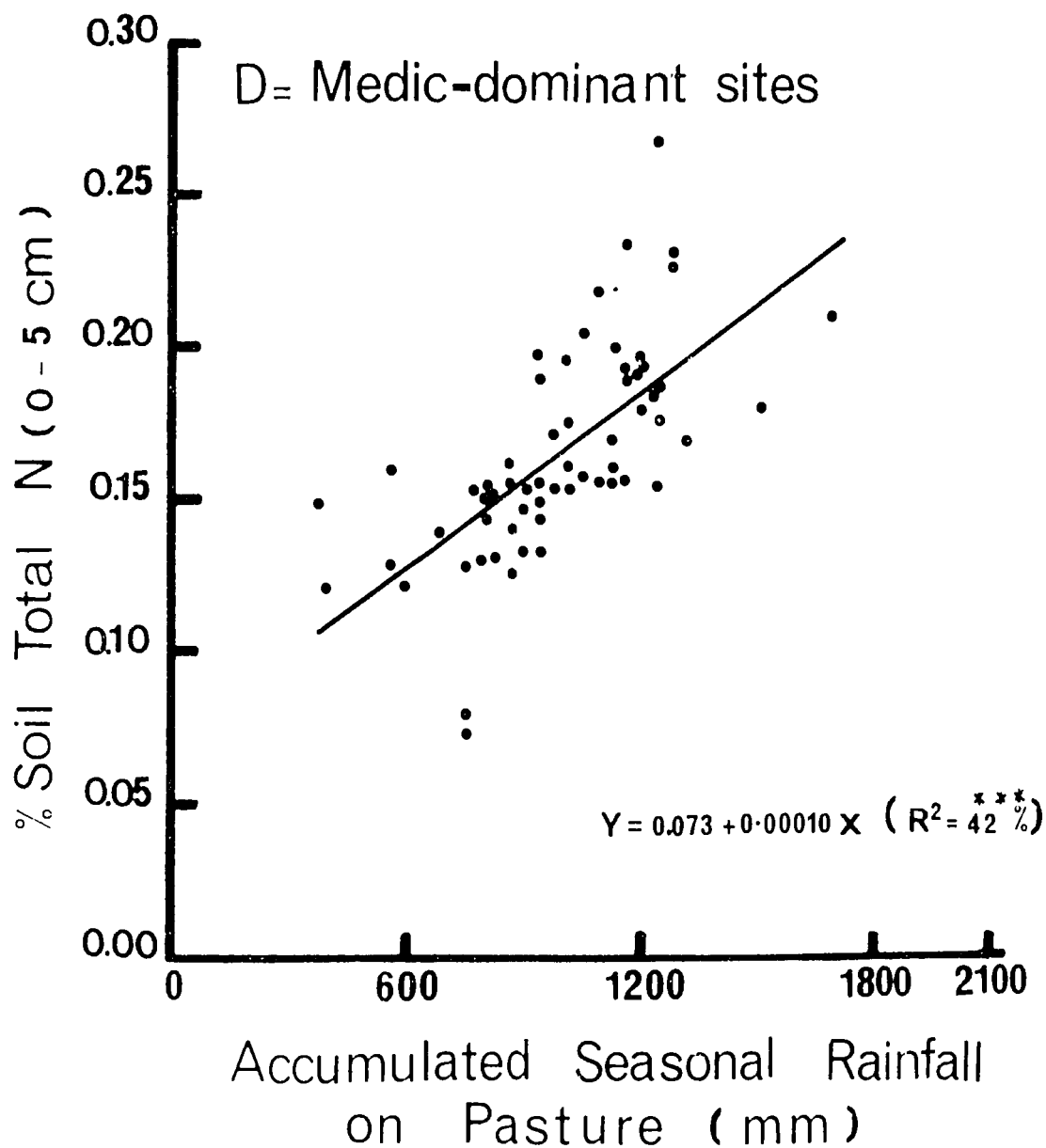


FIGURE 2. Relation between soil nitrogen level and rainfall-related growth of pasture legumes. (Dahmane, 1978)

Roles of Barley Diseases in Arid and Semi-Arid Environments

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Barley, in contrast to other crops, can be grown and gives some production under the severest stress conditions, particularly in regard to moisture and alkalinity. In spite of the adverse conditions in which barley is grown, diseases can still be important factors reducing production. Dew points are often attained even under desert conditions, and even short dew periods can be sufficient for ingress of many leaf pathogens. The barley in the concerned areas is grown during that seasonal part of the year most favorable to the crop as well as the disease pathogens.

Due to efforts of many people working in International Centers, or at least in International Agriculture (often funded through the auspices of the U.S. Agency for International Development), considerable progress has been made in achieving a better understanding of barley diseases. Much of the expanded program has occurred within the last 10 years. This has led to better control and should continue to further promote barley production in the more arid and semi-arid environments. The last workshop on barley, held in Rabat, Morocco, dealt with many ideas and approaches for improving barley. The reports and information to be given at this current meeting will contribute further to more knowledge and development of the number two crop in the dry areas.

Various approaches, such as the use of Preliminary Observation Nurseries and Regional Disease Trap Nurseries, along with associated research projects, have resulted in much information on the prevalence and severity of the many barley diseases. This information in turn has been used to direct efforts to further increase barley production through better disease control.

Barley Diseases

If an area having a general annual maximum limit of 400 mm precipitation is contemplated, the following diseases — based on a number of reports — may be considered. Of course, any one year may exceed the maximum limit based on long-term

averages and also (at least temporarily) affect the disease picture.

Helminthosporia

Using the old system of nomenclature, three species of *Helminthosporium* - *sativum* (spot blotch), *teres* (net blotch), and *gramineum* (stripe) are often prevalent and severe in certain areas. The fungus causing spot blotch also causes a dry land root rot which may be the more notable and debilitating under dry conditions. Selection for better yielding types may fortunately tend to select for more tolerant or resistant barley. Net blotch generally occurs wherever barley is grown, and is known to occur as a spot form as well, which can be easily confused with the true spot blotch. The stripe disease also occurs even under the driest conditions and is particularly noted where farmers use their own seed year after year.

Scald (*Rhynchosporium secalis*)

Scald (*Rhynchosporium secalis*) may occur over the general area, but is found particularly where temperatures during growing season are somewhat on the cool side. Scald is notably present in areas of Turkey and Syria, but also may occur in North Africa in some years.

Rusts (*Puccinia hordei*, *P. strüformis*, *P. graminis*)

Of the three rusts, *P. hordei* (leaf rust) is the most common and important. In addition to some overall distribution, it may occur in oases of the desert region of North Africa. The alternate host (*Ornithogallum*) is widely prevalent through some areas such as Tunisia, and may serve as an additional method for development of physiologic races. *P. strüformis* (stripe rust) is rather sporadic in occurrence, but can be a serious consideration under some conditions in some years. *P. graminis* is not often a problem in the drier areas of the Middle East.

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Smuts (*Ustilago hordei*, *V. nuda*, *V. nigra*)

Three smuts of barley (*Ustilago hordei*, *V. nuda*, and *V. nigra*) occur. Commonly called covered smut, loose smut, and black loose smut, respectively, they can be controlled by adequate seed treatment. Continual use of their own seed by farmers without seed treatment may allow increased prevalence of the smuts.

Powdery Mildew (*Erysiphe graminis*)

Powdery mildew is likely to appear throughout the designated area. Usually it is most prevalent during the earlier phases of the growing season and tends to phase out as higher temperatures prevail. Nevertheless, it is believed that the early infections can have a detrimental influence on the crop.

Barley Yellow Dwarf Virus

This virus disease, which can be vectored by several species of aphids, generally is present throughout the dry areas but varies from year-to-year depending on conditions for aphid multiplication. The Yd₂ genes give some tolerance, but the background of the pedigree influences the basic efficacy.

Bacterial Diseases

Two diseases caused by *Xanthomona translucens* and *Pseudomonas syringae* are possible, but are of minor importance overall. Seed industry control could exclude them.

Conclusion

The best control of many diseases of barley is through breeding for disease resistance. These aspects will be covered in other reports, but parents with low coefficients of infection when tested at many locations show promise. Most all species of the pathogens consist of different virulence types occurring throughout the area. Resistance studies need to include all possible resistance gene sources — whether major or minor in effect.

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The Influence of Water Potential on Plant-Microbe Interactions

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The osmotic strength of the environment is one of the factors which determines the ability of organisms to propagate in a given habitat. According to current understanding of microbial pathogenesis, the invasion of a host by a pathogen involves a set of staged genetic responses in which genes encoding proteins required for various aspects of the process are expressed sequentially throughout its entire course (DiRita & Mehelanos, 1989). Because of the limitations that water potential places on the proliferation of organisms, one might expect that osmolality would be an important constraint on interactions of pathogens with their hosts. In bacterial pathogens of animals, a number of virulence-associated genes have been shown to be under osmotic control (Bernardini *et al.*, 1990; Berry *et al.*, 1989; Chambers & Kunin, 1987; Dorman *et al.*, 1989; Dorman *et al.*, 1990; Galán & Curtiss, 1990). However, scant information exists on the influence of water potential on plant-microbe interactions.

All organisms, including fungi, vary greatly in their ability to grow in environments of various water potentials. There is some correlation between the water stress tolerance of fungi in their free-living states and their ability to parasitize plants at different water potentials. Thus, fungi which, in their free-living state, require high water potential for growth tend to cause plant diseases that are favored by wet conditions; conversely, fungi which can tolerate low water potential elicit diseases favored by dry conditions (Cook & Papendick, 1972). However, there are many exceptions to this generalization, and our understanding of the interaction between water potential and pathogenesis is in its infancy.

Cells of many organisms, ranging from bacteria (Csonka, 1989) to higher plants (Wyn-Jones & Gorham, 1983) and animals (Gilles *et al.*, 1987), accumulate the quaternary amine glycinebetaine (N,N,N-trimethylglycine) in response to high osmolality (i.e., low water potential). Two different, not necessarily mutually exclusive, functions have been proposed for this metabolite: (1) It may be a "compatible solute" which regulates the intracellular osmolality (Brown & Simpson, 1972); or (2) it may be a

stabilizer of proteins or other macromolecules in solutions of low water activity (Wyn-Jones & Gorham, 1983). That glycinebetaine contributes to the ability of organisms to tolerate conditions of low water potential was most clearly demonstrated by the observation that, when present in the growth media of *Escherichia coli* or other species of bacteria, this compound can overcome the inhibitory effects of high osmolality (Csonka, 1989).

There are two lines of experimental evidence that tie glycinebetaine to pathogenesis. Glycinebetaine has been found to be a growth stimulant in plant-free media for the pathogenic fungus *Fusarium graminearum*, the causative agent of wheat head blight (Strange *et al.*, 1974). However, no tests have been conducted to determine whether *F. graminearum* requires glycinebetaine for maximal growth rate regardless of the osmolality or whether, like *E. coli*, it is stimulated by this solute only under conditions of high osmolality. The anthers of wheat are much more susceptible to infection by *F. graminearum* than any of its other organs. Interestingly, wheat anthers have a very high content of glycinebetaine in comparison to other organs of this plant, which suggests that the tissue specificity of *F. graminearum* is likely to be the consequence of its dependency on glycinebetaine for optimal growth (Strange *et al.*, 1974).

The second connection between glycinebetaine and pathogenesis has been observed in *Agrobacterium tumefaciens*, the causative agent of crown gall in many species of dicotyledonous plants. During the infection of a host by this pathogen, a piece of DNA (the T-DNA), which encodes genes for the production of plant hormones and for the catabolism of nitrogenous compounds known as opines, is transferred from the bacterium to the plant cells and integrated into the nuclear DNA of the host (Ream, 1989). The infection process requires the transcriptional activation of the *A. tumefaciens vir* genes, which specify

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proteins required for the transfer of the T-DNA into the plant cell. Acetosyringone and similar phenolic molecules have been shown to be the inducing signals for the *vir* genes (Stachel *et al.*, 1985). Recently, however, Vernade *et al.* (1988) reported that glycinebetaine potentiated the acetosyringone-dependent induction of the *vir* genes in plant-free media. Once again, it is unclear whether the stimulatory effect of glycinebetaine in the induction of the *A. tumefaciens* *vir* genes is connected to its function as an osmoprotectant.

To date, the clearest example of regulation of plant-microbe interaction by water potential has been obtained with *A. tumefaciens* and *Rhizobium meliloti*. As Gram-negative bacteria, these organisms contain a cellular compartment known as the periplasm, located between the cytoplasmic membrane and the peptidoglycan cell wall. The periplasmic space contains high molecular weight oligosaccharides, known as membrane-derived oligosaccharides in *E. coli* (Kennedy, 1987), and β -1,2-glucans in *A. tumefaciens* and *R. meliloti* (Dylan, Helinski, & Ditta, 1990; Dylan, Nagpal, Helinski, & Ditta, 1990; Miller *et al.*, 1986). These solutes were found to be present at maximal levels in Gram-negative bacteria in media of low osmolality, and their synthesis was inhibited in media of high osmolality. Because of this osmotic control of their synthesis, the membrane-derived oligosaccharides and the β 1,2-glucans were proposed to regulate the osmolality of the periplasmic space (Kennedy, 1987; Miller *et al.*, 1986).

There are mutants both in *R. meliloti*, called *ndv* (Dylan, Helinski, & Ditta, 1990; Dylan, Nagpal, Helinski, & Ditta, 1990), and in *A. tumefaciens*, called *chvA* and *chvB* (Cangelosi *et al.*, 1990; Zorreguieta *et al.*, 1990), in which the synthesis of the periplasmic β -1,2-glucans is blocked. These mutants are also unable to infect plants. (In fact, they were originally identified on the basis of the non-infectious phenotype.) These mutants exhibit a growth impairment in plant-free media of low osmolality, but not in media of high osmolality, providing strong evidence for the importance of β -1,2-glucans in osmoregulation.

Other than these few examples, little is known about the interaction between pathogenesis and water potential. However, because of the importance of osmoregulation in cell physiology, this area is likely to be the subject of keen investigation in the future.

Acknowledgements

I thank Drs. G. Cangelosi, G. Ditta, and A. Hanson for helpful discussions. My laboratory work

in osmoregulation was funded by grants from the Corporation for Science and Technology, the U.S. Department of Agriculture (#87 CRCR-1-2495), and the U.S. Public Health Service (#R01-GM-319-4401).

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Stability of Stress Resistance to Biotic and Abiotic Stress Factors

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Stress

Nearly all organisms have to live and survive in an environment that is heterogeneous in time (weather, climate, other organisms) and space (topography, soil, other organisms). This means that organisms cannot be optimally adapted all the time; they must be under stress at least part of the time.

Stress can be described as the direct effect on the organism, when it is exposed to a detrimental factor (stress factor) for some time, through which the organism cannot function optimally. As a result of the stress, damage develops.

Individuals experiencing the least stress have the greatest chance to survive. The survival of an individual is a function of the ability to *avoid*, to *resist*, or to *tolerate* the stress factors or to *recover* from the consequences of the stress factors. The winterhardiness of winter wheat consists of two components: tolerance to freezing temperatures (no damage incurred), and ability to recover from damage suffered by the low temperatures (*Table 1*). Tolerance to freezing temperatures is the most important component of the two; the winterhardiness never deviates more than half a point from the cold tolerance value.

Stress in agriculture is always present. Boyer (1982) showed this very convincingly. For each of a number of crops, he compared the highest farm yields ever realized in the U.S.A. with the mean yields in the U.S.A. The highest yield is a (lowest) estimate of the genetic potential of the crop. For maize, the highest farm yield recorded was 19.3 ton/ha, and the country-wide average 4.6 ton/ha. Averaged over the major crops, the mean yields were only 25% of the highest yields. This reduction of 75%, Boyer estimated, was due to pests, diseases and weeds for only 11% and to abiotic constraints for 64%. Due to resistance breeding, pesticides, and agronomic measures, the biotic stresses are reasonably under control. With abiotic stress, the situation is considerably less favourable. This is valid in a country with an advanced agriculture. In developing countries, the realized yield may be only 10% or less of the genetic potential, with both the biotic and abiotic stresses causing large yield losses.

Stress Resistance

Agronomy and breeding both try to reduce the stress complex to which the crop is exposed. The former does so by adapting the environment to the potentials of the crop (irrigation, fertilization, crop protection, greenhouses), while the latter aims at adapting the crop genetically to the environmental constraints (resistance to animal parasites, to pathogens, and to various kinds of abiotic stress).

The term "resistance" is used rather ambiguously. Against pathogens, it is used in its true sense, i.e., to resist the stress factor. The pathogen is hindered in its growth and development. Against animal parasites, resistance is used in a much wider sense, including avoidance (antixenose, through disturbance of the animal's behaviour), true resistance (antibiosis, through hindering the growth and development of the parasite), tolerance, and recovery. Resistance to abiotic stress, too, has a wide meaning comprising avoidance, true resistance, tolerance, and recovery mechanisms.

The farmer (and so the breeder) desires cultivars that are damaged as little as possible by the stress factor to which they are exposed. Whether the reduced damage comes from avoidance, resistance, tolerance, or recovery mechanisms, or from a combination of mechanisms, is often unclear and difficult to assess. Because of the difficulty in assessing the precise mechanisms behind a reduced damage when exposed to stress, the term "resistance" is used here in a wide sense including avoidance, true resistance, tolerance, and recovery — resistance *sensu lato* (s.l.).

Stability of Stress Resistance

The ideal cultivar has a genetic potential for high performance, which is expressed under a wide range of environmental constraints, i.e., a stable performance at a high level. This is possible only if the cultivar carries resistance to the various stress factors

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that may occur in the area where it is grown. Thus, stability of stress resistance is essential to obtain a stable performance. Unfortunately, the concept "stability of stress resistance" is difficult to define. As with any other trait, it is the expression of the resistance that can vary so greatly. So with stability of resistance, the stability of the expression of resistance is meant. The larger the variation in its expression when exposed to the stress factor, the smaller its stability.

The expression of resistance to a stress factor may change because of: (1) a change in the stress factor itself, (2) an interaction with a non-stress environmental factor, or (3) an interaction with another stress factor. Examples may illustrate this.

(1) The expression of resistance to a pathogen can disappear when the pathogen population changes, i.e., when a new race, pathotype or biotype, neutralizing the resistance, appears.

(2) In the presence of the stress factor, the expression of the resistance to the stress may vary with the environment. The winter hardiness of winter barley is not or only poorly expressed if the plants have not been acclimatized. Resistances to various pathogens are temperature dependent. Partial resistance of wheat to brown rust, *Puccinia recondita* f.sp. *tritici*, is poorly expressed at very high temperatures and very well expressed at low temperatures.

(3) Interactions between stress factors often occur and may not even be recognized as such. Drought resistance of a cultivar may be reduced strongly if affected by root knot nematodes.

Here the stability of resistance to biotic and abiotic stress is discussed, the former only summarily as so much has already been written about it. The latter is discussed in more detail because of the importance of abiotic stress (Boyer, 1982), especially in arid and semi-arid environments. When discussing the stability of resistance to abiotic stress factors, the problem arises that the stress factor itself is often so unstable or erratic in its occurrence, making it impossible to separate the variation in stability of resistance from the variation in the exposure to the stress factor. Because of this, a discussion of the stability of abiotic stress resistance is largely a discussion about the large and unpredictable variation in exposure to the stress factor and its consequences for breeding for resistance.

Another aspect may and often does interfere with the proper assessment of the stability of resistance to abiotic stress. With some very important stress factors, the resistance to the stress is difficult

to separate from another trait, the yield performance *per se*. With drought and salinity, the stress resistance is measured through the yield performance under drought conditions, linking stress resistance with yield performance *per se*. Therefore, this must be discussed as well.

Stability of Biotic Stress

The expression of resistance to parasites may change due to: (1) the adaptation by the parasite population, (2) an interaction with the abiotic environment, or (3) an interaction with another biotic stress factor.

Adaptation by the Parasite Population

The ability of parasites, especially some groups of fungal pathogens, to adapt to introduced major gene resistances has been discussed in great detail by many scientists. In barley, powdery mildew (*Erysiphe graminis* f.sp. *hordei*) forms a clear example. Durability of resistance, determined by the rate of response in the parasite population, is influenced by various factors such as:

The genetics of the resistance. Resistances that evoke adaptation in the parasite population are nearly always of the major gene type. More complex resistances tend to be much more durable.

The farming situation. The rapid "breakdown" of race-specific major resistance genes predominantly occurs in major crops, i.e., when a crop occurs frequently over a large area. In Western Europe, major gene resistance to yellow rust, leaf rust, and powdery mildew in wheat becomes ineffective due to development of new races of the pathogen within a few years in most cases. Wheat is a major crop. In contrast, the major gene resistance in flax to flax rust has remained effective in most cultivars for the last decades. Flax has become a minor crop and all cultivars are resistant. There is hardly any inoculum present (Parlevliet, 1990).

The parasite species. The rate at which parasite populations adapt to the resistance in the host varies greatly among the parasite groups. Rapid adaptation in parasite populations occurs predominantly in biotrophic (rust, smuts, bunts, powdery mildew of cereals) and hemi-biotrophic (scald in barley) fungi (Parlevliet, 1990).

An Interaction with the Abiotic Environment

A resistance to a pathogen is only effective in a specific environment. Browder (1985) says this very

clearly. Resistance of a host only exists when the host is exposed to the corresponding specific pathogen race (carrying the avirulence factor for the resistance factor in the host) in the required specific environment. Any deviation, either in the avirulence factor of the pathogen or in the abiotic environment, results in susceptibility. Temperature, especially, is a factor in the abiotic environment that can influence profoundly the expression of the resistance to pathogens. But also light intensity, day length, relative humidity, soil fertility, plant age, and development stage may interfere with the level of expression of the resistance (Tingey & Singh, 1980).

An Interaction with Another Biotic Stress Factor

Plants normally are affected by more than one parasite. Resistance to one parasite may be affected by the presence of another parasite. Barley plants become more susceptible to barley leaf rust when affected by barley yellow dwarf virus. Resistance to vascular wilt causing pathogens, such as *Verticillium albo-atrum* and several formae speciales of *Fusarium oxysporum*, is often strongly reduced when the root system is invaded by root knot nematodes.

Stability of Abiotic Stress — General Aspects

In the field, a crop is exposed to a great variety of variables that may hamper its growth and development. Those variables of a non-biological nature can be collectively indicated as abiotic stress factors. In this way, stress is used in a broad sense; any damaging factor is called a stress factor. Water logging, drought, acid soil, frost, wind, hail, and heat can be abiotic stress factors. In a number of cases, the stress can be taken away very efficiently through technological or agronomic means such as drainage, irrigation, liming, greenhouses, etc. Despite such developments, a very large acreage of our food crops is still exposed to a variety of abiotic stress factors, considerably reducing the potential yields — as Boyer (1982) demonstrated.

Crops vary considerably in resistance *s.l.* to stress. For instance, wheat and barley vary greatly in winterhardiness and in tolerance to acid soils. The modern breeder wishes to accumulate resistance to several stress factors and to do so in a relatively short time. Asking for efficient screening methods for all the selection criteria involved is a tremendous task.

For rapid progress in breeding for abiotic stress resistance, the breeder must: (1) know the stress factor; (2) be able to manipulate the intensity, duration, and uniformity of exposure to the stress factor; and (3) be able to recognize and assess the resulting stress or stress damage accurately. If one or more of these requirements is only partially met, or not met at all, the screening becomes less efficient, i.e., the fewer the requirements met, the less efficiency.

Some stress factors, for instance, are difficult to manipulate (wind, drought, severity of winters). Stress damage can be difficult to measure as it must be measured through the resulting yield loss. Yield loss is a difference between yield under stress and yield in the absence of that stress. Yield itself harbours a large error, and a difference between two yield estimates is even less accurate.

The number of abiotic stress factors for which resistance or tolerance is desired is quite large and may vary from region to region. Here a number of stress factors relevant in cereal breeding are discussed. The stress factors are chosen to represent the whole range of difficulties breeders may meet when breeding for adaptability to abiotic stress factors. It is possible to categorize the stress factors into three groups: (1) the stress factor produces an undesirable reaction, (2) the stress factor suppresses desirable reactions, and (3) stress is present in the absence of identifiable stress factors.

(1) The stress factor induces or results in an undesirable reaction, such as the sprouting of the grains in the ear due to humid weather conditions during grain ripening. Other examples include lodging in wheat and barley as a result of rain and wind, and breaking off of the barley ears in areas where the harvest is often postponed by bad weather.

(2) Desirable reactions are suppressed by the stress factor. This mostly pertains to the suppression of growth, leading to a reduced biomass and yield. Drought, acid soils, salinity, freezing spells, and heat are examples of such stress factors.

(3) Even if no specific stress factors can be identified, stress is normally present. If cultivars are tested over years and locations, the mean yields vary with the environments. These differences are often considerable. Therefore, stress is present, but as a complex of unidentifiable stress factors. By testing cultivars over a range of years and locations, the breeder can and does select for cultivars with a broad adaptability, i.e., for cultivars resistant to this complex of unidentified stress factors.

Whether the breeder will be successful in selecting resistant cultivars depends on the uniformity of exposure in time and space of the breeding populations to the stress factor and on the heritability of the stress resistance. This is summarized in *Table 2* for a number of abiotic stress factors that play an important role in cereals. The intensity and duration of most abiotic stresses vary greatly in time, within and between seasons. Soil-borne abiotic stress factors, such as salt or acidity, tend to occur very heterogeneous in space (within and between fields).

Taking all this heterogeneity together means that a uniform exposure to the stress factor at the desired intensity and for a given period remains Utopia for the breeder. This erratic and heterogeneous occurrence of the stress factor means that the assessment of resistance to the stress factor is far from easy. If the resistance is inherited in a fairly simple way, the heritability may still be reasonable (acid soil tolerance, lodging resistance). In the case of a highly complex inheritance, the heritability tends to be very low (drought resistance, broad adaptability).

Abiotic Stress Factors Causing Undesirable Side Effects

Undesirable reactions are often induced by specific weather conditions. Moist and cool weather during grain ripening may induce sprouting. Rain and wind, especially together, can cause lodging after heading and breaking off of barley ears after maturing. The undesirable effects are fairly easy to observe and the stress factor tends to occur uniformly over the experimental field, which is favourable for a representative assessment of the resistance to the undesirable effect. However, the frequency, duration, and intensity of the stress vary strongly within and between seasons and between locations, reducing the reliability of the assessment considerably. A screening test has been developed only for sprouting. Ears are taken into a cool and moist room for a defined period. The results differ, however, because acclimatization of the maturing spikes plays a considerable role. Sprouting, and thus the resistance to sprouting, depends on the environmental conditions preceding the sprouting inducing conditions. Because these conditions are not well known, a good screening test is difficult to develop.

Obtaining a satisfactory assessment for these traits requires evaluating the entries over a few years and locations — at least, conditions which normally occur in a selection program.

Abiotic Stress Factors Suppressing Desirable Effects

Through various measures, the farmer tries to stimulate the biomass production and yield. To maximize effects, the crop should grow unhindered all the time. Several abiotic stress factors may hamper this growth process for shorter or longer periods, with reduced yields as a consequence.

Here four abiotic stress factors with quite different problems are discussed: (1) acid soils, (2) winter-hardiness in barley and wheat, (3) salt tolerance, and (4) drought resistance.

Acid Soils

Large areas in the world have low pH-values. The root growth of sensitive crops or cultivars is reduced, as is the total biomass production and grain yield. An excess of Al in such acid soils intensifies the stress considerably (Al-toxicity). The ranking order for tolerance to acid soils among the small cereals is from barley (least tolerant), wheat, rye, to oats (most tolerant). Drought increases the acidity and Al-stress considerably. The pH-KCl value varies during the season and across fields. The variation within fields can be especially large and is associated with variations in water holding capacity, actual water contents, and differences in soil structure and soil type. These variations within fields often cause a large experimental error in the breeding populations under selection. Therefore, selection in the field is not very reliable.

Fortunately, there is a fairly satisfactory screening test, developed by Mesdag and Balkema-Boomstra (1984). Acid soil, peat, and some H_2SO_4 are mixed to give a soil with a pH-KCl of about 3.6. Wheat screening requires the addition of slightly more H_2SO_4 than for barley. Flats filled with this soil are sown with the entries to be screened. In each flat, two check cultivars are sown. For barley, Bavaria (very tolerant) and Alfor (very sensitive) can be used, and for wheat, Colonnais (very tolerant) and Thatcher (very sensitive). Ten (barley) and 15 (wheat) days from sowing, the root system is assessed in relation to the controls on a scale of 1 (Alfor, Thatcher) to 9 (Bavaria, Colonnais). The test conditions are much more severe than the reality in the field, but the exposure is much shorter. The screening results agreed very well with those from the field and with experience gained in practice.

In both barley and wheat, the inheritance of the tolerance to low pH is fairly simple. The cultivars

differed for only one or a few genes with additive effects (Mesdag & Balkema-Boomstra, 1984).

Screening for acidic, Al-rich soils can be done even in the laboratory. Cesati *et al.* (1988) describe a method used by CIMMYT to screen wheat entries for tolerance to Al-toxicity. Sterilized, soaked seeds are placed on wet filter paper in petri dishes. After a few days, the sprouted seeds are placed on a construction floating on a nutrient solution. After 32 hours in the nutrient solution, they are transferred to a nutrient solution containing 46 ppm Al and having a pH of 4.0. The exposure to Al lasts 17 hours at 25°C, after which the seedlings are washed and returned to the nutrient solution without Al. Tolerant entries show a clear regrowth of the roots after the Al exposure, while the sensitive ones do not resume root growth. Table 3 shows some data from a similar test. The screening test assessment agrees fairly well with the field results. All cultivars that react sensitively in the field show no regrowth at 6 mg/l Al. All tolerant cultivars show a variable regrowth at 6 mg/l Al. But it is not always possible to distinguish slightly tolerant cultivars from sensitive ones, or moderately tolerant from tolerant cultivars. As a screening, however, it is a useful approach because the moderately tolerant and tolerant entries are clearly recognized. Each screening test uses a well-known sensitive and tolerant cultivar as a control.

Breeding barley and wheat cultivars suitable for acidic soils is quite possible. Through the screening tests, the tolerant and moderately tolerant entries can be selected. These should be field tested to ensure that the tolerance is of the required level and is embedded in genotypes of a suitable agronomic performance.

Winterhardiness in Barley and Wheat

The small cereals vary considerably in the intensity of cold they can endure. Rye is the most winter-hardy small cereal, followed by wheat and barley. Oat is the least winterhardy. Within each species, large differences in winterhardiness exist. Winterhardiness is a complex trait (as shown in Table 1), but cold tolerance is the most important component.

The stress factor is extremely variable, especially in time. The intensity, duration, and frequency of cold vary greatly between winters. Presence or absence of snow can be a decisive factor, whereby the thickness of the snow cover is often highly variable within the experimental fields due to wind and slope. The stability of winterhardiness is, to a large extent, affected by its preconditioning, by the acclimatization

process preceding the cold. Due to the erratic occurrence of cold and the associated variation in acclimatization when the cold hits, the results of screening for winterhardiness in the field are rather inaccurate. Results over at least several locations and several years are needed for a good assessment. To escape the problems encountered in field testing, screening tests have been developed in which the entries to be screened are sown in flats or shallow containers. The seedlings, after some acclimatization — usually outdoors in early winter or late autumn, or at temperatures close to zero °C for some time — are exposed to low temperatures (barley -13°C, wheat -15° or -16°C) for 24 hours. The percentage of seedlings surviving this treatment is a measure of winterhardiness. Unfortunately, the acclimatization is of such importance that it has not been possible to develop a satisfactory screening test. The results tend to vary from one test to the other. Only the really cold sensitive entries can be removed with certainty.

A single test is therefore insufficient to classify entries in the right winterhardiness class. The entries must be exposed repeatedly to such a screening test, whereby the acclimatization treatments preceding the cold exposure are varied, in order to obtain a more reliable assessment. This was clearly demonstrated by Hoberg and Finck (1984) in the case of barley.

Salt Tolerance

Injury due to salt in the soil is a widespread and old problem, especially in arid and semi-arid regions. High salt concentrations in the soil water create high osmotic pressures, reducing the availability of water to the plants. At the same time, specific ions such as sodium and chloride may prove toxic at higher concentrations.

Of the cereals, barley is the most tolerant to salty conditions. The importance of having salt tolerant cultivars has been discussed for several decades. The fact that no truly tolerant cultivars have been issued until now suggests that it must be very difficult to produce cultivars with a desirable agronomic performance together with a significant salt tolerance.

There are several reasons why progress has been virtually zero:

(1) Saline soils are exceedingly variable in both the kinds of salts present and in their concentration. The cation exchange properties of soils add more complexity, as do spatial and temporal variations in all these features (Epstein *et al.*, 1980).

(2) Tolerance to salinity is almost certainly complexly inherited.

(3) Tolerance must be measured either as a reduction in loss of biomass or as a reduction in yield loss. Biomass and yield are not easy to assess accurately.

(4) The damage caused by some salinity is extremely large. At salinity levels 40% of that of seawater, the biomass in wheat was reduced to about 9% for the most tolerant and to about 2% for the sensitive entries (Kingsbury & Epstein, 1984). Although differences in tolerance are highly significant, the cultivar effects are small compared to the total damage. Unusually high levels of tolerance are needed to prevent such a large damage.

Heterogeneity of salinity. Epstein *et al.* (1980) stated that the nature and intensity of the stress varies widely, spatially, and temporally, which means that what is selected in one salty environment may not be adapted to another. Even within one field, the heterogeneity is very high (as shown in Table 4), so screening for salt tolerance in the field is rather inefficient. To screen for salt tolerance, the entries must be exposed uniformly over a given period of time to a predetermined salinity stress. This is possible, in principle, through salinized solution cultures (hydroponics) or through sand cultures watered with a standardized salinized solution. As salt tolerance probably is a complex trait, it is unlikely that seedling screening only will give a representative result. So exposure should be during most of the life cycle of the plant, requiring considerable areas with such facilities. Other screening methods have been tested as well — without encouraging results. Ray (1988) concluded that, at present, there is no screening method available that indicates salt tolerance quickly and accurately.

Even if such a method were to be developed, only the tolerance to salt would be assessed. No information would be obtained about its agronomic performance, especially yield under non-saline conditions. And it is essential that salt-tolerant cultivars also yield good at non-saline conditions (Shannon & Qualset, 1984; Richards, 1983), as the salinity within salty fields varies greatly — from almost zero to levels where no crop can grow. This means that if it is decided to select for salt tolerance, the breeder must select for both salt tolerance and yield potential under non-stress conditions. A preliminary tolerance test to separate the salt-tolerant from the salt-sensitive genotypes must be followed by extensive yield testing under non-stress conditions of the tolerant entries.

Tolerance to salinity. Within crops, and also within barley and wheat, genotypes clearly differ in degree of tolerance to salinity (Epstein *et al.*, 1980; Kingsbury & Epstein, 1984; Richards *et al.*, 1987). Selection for salt tolerance is possible if a good screening test is available, but such a screening method has not yet been developed. The tolerance cannot be measured, as with acidic soils, through the effect on root growth or another trait directly affected by the saline conditions. It is the reduction in grain yield which is indicative of the tolerance. The higher the tolerance, the smaller the reduction compared to yield in non-saline conditions. This makes it automatically a complex trait, whereby the exposure to the saline conditions must last over the entire growth cycle of the plant or crop.

In some crops, cell cultures are exposed to saline conditions, an attractively simple test. Apart from the fact that regeneration still forms a problem in small cereals, it is not yet clear how useful cell culture testing will become. It is still unclear whether salt tolerance at the cell culture level and salt tolerance of the plant or crop are identical or similar traits. The reports are as yet conflicting (Stavarek & Rains, 1983). Also, the somaclonal variation going together with regenerated cell cultures may cause problems. Here, too, the tolerant lines must be field tested extensively to assess the agronomic performance under non-stress conditions.

Is tolerance to salinity needed? The extreme heterogeneity of the salinity in saline fields and the very rapid loss of yield performance create a special situation. Crops grown on saline fields are exposed to levels of salinity varying from close to zero, to too high for crop growth (Shannon & Qualset, 1984). The best genotype for such conditions may not be a cultivar with the highest salt tolerance level, but a genotype that yields very well at non-saline conditions and reasonably well at the high saline patches. Richards (1983) recognized and investigated this. He estimated the percentage of land in seven salinity classes (Table 4) of an extremely saline, a saline, and a non-saline field. From another saline field carrying a yield experiment with 16 barley cultivars and lines with varying levels of salt tolerance in six replicates, he obtained grain yields in relation to the salinity. Per genotype, about 20 quadrats of 0.37 m² were chosen, ranging from areas with visually no observable damage to areas where grain yield was greatly affected. Of these quadrats, the salinity in dS/m and the grain yield in g/m² were measured. From the strong negative linear relationship between grain

yield and salinity, the grain yield per salinity class (*Table 4*) was estimated averaged over cultivars. These yields were used to estimate barley yields on the extremely salty, salty, and non-salty fields to provide the data in *Table 4*. The saline fields appeared very heterogeneous, forming a mosaic with a considerable part not being salty, while at neighbouring patches no crop could grow. The areas in the fields above 20 dS/m did not contribute to the field. The greater part of the yield (over 80%) was produced on the non-saline or slightly saline patches. The yields used in this calculation represent the yield of barley genotypes that on average can be considered moderately tolerant to saline conditions.

What would be the best breeding strategy to improve the barley yields on such saline soils? *Table 5* depicts four improved cultivars derived from breeding for higher yield under non-saline conditions or under uniform very saline conditions. An increase of yielding potential of 10% without change of the level of salt tolerance would give yields as shown in *Table 5*. At all levels of salinity, the yields increase with 10%. This is not very likely to occur. Rosielle and Hamblin (1981) stated that selection for stress tolerance is expected to produce a negatively correlated response in mean yields in non-stressed environments. The reverse is equally probable. Starting from the on average moderately tolerant population selection for high yielding potential *per se* is likely to lead to some loss in tolerance to salty conditions (high yielding-2, *Table 6*). Selection for a high level of salt tolerance without losing yield potential (very tolerant-1) is therefore also not likely to occur. More realistic in such a case will be the very tolerant-2 type of cultivar in *Table 5*. Comparing the four improvement situations, it is quite clear that only increasing the tolerance level, even if it is very considerable (two-fold at the 16-20 dS/m level of salinity), is inferior to increasing the yield under non-saline conditions. This is primarily due to the greater part of the yield being produced on the non-saline or slightly saline patches of saline fields.

This poses the important question, suggested by Richards (1983), as to whether it is useful to select for salt tolerance even if a suitable screening method were available. Richards' data clearly indicate that selection under non-stress conditions is to be preferred. In time, progress will be better, especially because selection for yield under saline conditions is far more tedious than under non-stress conditions. The h^2 for yield under severe stress is much lower than under optimal growth conditions. But even if

selection for tolerance were not so tedious, selection should be directed at the non- or slightly saline conditions because the greater part of the yield is produced on such patches.

The decision not to select for salt tolerance, but for high yield potential *per se*, with possibly a removal of only the really salt-sensitive entries, is of such an importance that this aspect should be investigated more thoroughly.

Drought Resistance

For continued growth and development of the crop, there should be sufficient water available at all times. This is often not the case unless man interferes by *f.i.* irrigation. The availability of water depends on various factors. The amount and distribution of precipitation is of prime importance, but the water-holding capacity and the runoff of the soil (soil type and soil depth) also are of considerable effect. Evaporation is another factor of importance. These combined factors determine the intensity and duration of the drought stress experienced by the crop.

If the breeder wishes to select for differences in resistance, the stress factor should occur homogeneously over the field at a time considered representative for the occurrence of the drought stress. However, this is very difficult to realize as the precipitation in many regions of the world is very erratic.

At Kibwezi, Kenya, for instance, the average rainfall is 645 mm, but varied in a 40-year period from 245 to 1200 mm. The rainfall shows two peaks, one in November-December with an average of 310 mm, and one in March-April with an average 210 mm. Either one or both peaks may fail. The distribution of the rainfall within one rainy season may vary from well-distributed to a few heavy rainstorms widely separated in time.

So between and within growing seasons, the natural rainfall shows a high heterogeneity. In many cases, there is no clear representative period and intensity of the drought stress. It is possible, though, to distinguish two types of drought stress: the drought stress tends to occur at and intensify towards the end of the growing season (terminal drought), or it can occur anywhere during the growing period (intermittent drought).

Even within a field where erratic rainfall is considered the same, the drought stress may vary considerably due to differences in soil depth and runoff caused by differences in slope.

Therefore, the start, intensity, and duration of the drought stress vary from season to season and from

location to location. The drought stress may occur at or just after germination, during the seedling stages, during tillering, during flowering, or during the grain filling period. The sensitivity of the crop to the drought stress varies with the development stage, but is also dependent on the growth history of the crop preceding the drought stress (acclimatization). In such situations, genotype x environment interactions (genotype x drought stress conditions) often play a significant role.

Apart from the difficulties in obtaining a representative and uniform drought stress exposure, the breeder faces the problem of measuring drought stress. In cereals, drought stress is measured through grain yield, as with salt tolerance. This only increases the problems for a breeder who wishes to select efficiently for drought resistance.

But, as with salt tolerance, it is not only drought resistance that is desired. Because drought stress varies from year to year and from location to location, one cannot select for resistance to a given drought stress. A cultivar adapted to a certain region must be yielding good relative to other cultivars at various levels of drought stress, from mild to severe levels.

With salt tolerance, it is at least possible to measure the salinity in dS/m. With drought stress, however, it is not really possible to measure the drought in the soil. So only the result, a certain degree of yield loss, can be used as a measure of the drought stress. Cultivars with a smaller yield loss are then considered more resistant to the drought stress than the average cultivar.

Table 6 illustrates some problems in measuring drought stress and the resistance to drought. In this assumed situation, a large number of cultivars are yield tested at a very dry location over several years. Five treatments are applied each year: full irrigation (I), no irrigation (V), and partial irrigation (II to IV). The mean yields over the years of the five treatments, averaged over all cultivars, could be seen as representing the drought stress — zero in treatment I and most severe in treatment V. The yield reductions due to drought stress range from 24% to 65% for treatments II to IV. The resistance of a cultivar can be taken as the deviation from this average pattern. Cultivars A and B are less resistant than the average cultivar; their yields drop faster with increased drought stress than the average. Cultivars C and D show an above-average resistance; their yields drop considerably slower. D is the most resistant cultivar.

How can the level of resistance be expressed in a simple figure? This can be accomplished by taking

the ratio of yield under stress to yield without stress. If environments V and I are used, A and B are equally susceptible to drought, the ratio being 0.30. C and D are considerably more resistant, D with a ratio of 0.50, slightly more so than C with 0.45. In this case, the information of only one stress environment is used. By using the regression coefficient of the cultivar effects on the environment index (the yields averaged over all cultivars per environment), all available information is used. The higher the regression coefficient, the stronger the cultivar reacts to the drought stress. The ranking order from susceptible to resistant is A, B, C, and D. The regression coefficient, using more information, seems the more appropriate parameter to represent the drought resistance, provided the drought stress and the resistance to the drought stress are linearly related.

However, the data of cultivar E create a problem. According to E's regression coefficient, it is less drought resistant than D, but it outyields this cultivar at all environments with 24%, including the most severely stressed environment. If it outyields cultivar D even in the most drought stressed environment, it cannot be less drought resistant than D. This problem was recognized by Fisher and Maurer (1978), who observed that the higher yielding cultivars tend to have a higher regression coefficient. This is easily explained if one realizes that biological yield should be viewed within a multiplicative system rather than in an additive one; the regression coefficient as shown in Table 6 is based on additive effects.

To meet this problem, Fisher and Maurer (1978) developed the *drought susceptibility index* (S).

$$S = \frac{Y_p - Y_d}{Y_p} \times \frac{X_p}{X_p - X_d}$$

where Y is the yield of the cultivar of which S is calculated and X is the mean yield of all cultivars present in the same yield experiment. The number of cultivars should not be too small, and preferably a random sample. Y_p and X_p represent the yields under non-drought stress conditions (the potential yield), and Y_d and X_d the yields under drought stress.

When the S-values are compared, a much better assessment of the true drought tolerance is obtained than with the regression coefficient (Table 6).

In this assumed situation, cultivar E is not a very realistic example, but the other four do represent a realistic situation. Rosielle and Hamblin (1981) concluded that yield potential and stress resistance can be expected to be negatively associated. Parlevliet (1988) indicated that this is the case for oats in The

Netherlands for yield potential and drought resistance. The breeder, therefore, must try to find a compromise between the yield potential and the drought resistance. If he has to choose between the cultivars A to D of *Table 6*, his choice depends on the mean and range in drought stress that occur in the region for which he is breeding. If environments II and III tend to represent the region, A is the obvious choice; if IV and V are more representative, C and D are the likely candidates.

The data provided by Edhaie and Waines (1989) clearly show the above mentioned problems. They compared seven spring wheats insensitive to photoperiod. Three genotypes were lines selected from Southwest Iranian landraces adapted to terminal drought stress conditions. The other four were recently bred cultivars; three were selected in Southwest Iran and the fourth was the Californian cultivar Anza. The seven genotypes were tested in six environments with different drought stress levels, ranging from no stress to severe. These environments were obtained through differential irrigation and different sowing dates in two years at Moreno, California, a location with terminal drought as in Iran. They applied the Finlay and Wilkinson (1963) model, but without a logarithmic transformation. With these untransformed data, the three Iranian landrace lines had low regression coefficients. *Table 7* shows the data for the two highest yielding cultivars and for two of the landrace lines.

Edhaie and Waines (1989) concluded that the landrace lines were more drought resistant because of the lower regression coefficient. A second conclusion was that Anza and Sholeh are the more desirable cultivars in even the severely stressed environments because of their high yielding ability. The latter conclusion is difficult to refute, but the first conclusion is less certain. By not using a logarithmic transformation, one assumes implicitly additivity of yield effects or, in other words, a change from 1.0 to 2.0 ton/ha is the same as from 6.0 to 7.0 ton/ha. Biologically, this makes little sense. If the yields of the four cultivars/lines in Edhaie and Waines' experiment had been *ln*-transformed before the regression coefficients had been calculated, another conclusion would have emerged (*Table 7, columns 6, 7, 8*); the Iranian landrace lines would not have appeared more drought resistant, and Anza certainly would not have been classified as drought susceptible.

The drought susceptibility index (S), gives a ranking similar to the regression coefficient after *ln*-transformation, but its discriminative power seems

somewhat less. The best parameter for expressing the drought resistance, therefore, seems to be the drought susceptibility index (S). The lower it is, the higher the resistance. A regression coefficient based on *ln*-transformed yield data would be even better because of its greater discriminative power, but one needs data from a fair number of different drought stress environments, which are not always available.

In either case, the assessment is laborious. It requires a lot of field testing to obtain a sufficiently accurate S-estimate. This cannot be done with thousands of entries, which restricts its use to the later generations of selections when a large part of the entries have already been removed for other reasons.

Despite the problems associated with the selection of genotypes adapted to drought prone areas, progress has been made. This is illustrated by Perry and D'Antuono (1989), who compared wheat cultivars introduced into the wheat belt of Western Australia between 1860 and 1982. These cultivars were tested in 20 environments (years and locations). The yields increased, from the oldest to the most recent, from 1.0 to 1.6 ton/ha. The regression coefficient of cultivar means on environmental indices (*see Table 6*) was higher for modern than for old cultivars. This suggests a decrease in drought resistance despite an increased yield performance over all environments of the modern cultivars. Here again, *ln*-transformation of the data would remove the greater part of the differences in regression coefficients. Apparently, the majority of the increased yield performance of the modern wheat cultivars has come from an increase in yield potential rather than from an increased drought resistance.

This raises a question similar to the one discussed in relation to tolerance to salinity. Should one breed for yield potential increases predominantly, or should one emphasize the drought resistance when selecting for drought stressed environments?

This depends on the average and range of the drought stress in the region. One could envisage the Y_p to be the result of traits that affect yield under all conditions and of traits that are desirable under non-stress conditions and undesirable under drought stress conditions. The Y_d is then the result of the same traits that affect yield under all conditions, and of traits that are specifically desirable under drought stress conditions and undesirable under non-stress conditions. The farther Y_p and Y_d are apart, the more the situation-specific traits become prevalent. For moderately stressed environments, the selection might favor the selection of Y_p , but for severely

stressed environments, one should probably try to increase the drought resistance. The barley data of Ceccarelli (1987) support this view.

Yield testing, especially under drought stress, is very inaccurate, and so assessment of drought resistance is equally inaccurate. It would ease the work of the breeder if he could apply indirect selection. For this purpose, one or more traits that are well correlated with drought resistance but with a considerably higher heritability are needed. Much research in various crops has been carried out, but the results are not encouraging. There is no single trait that can be used for this purpose. In a few cases, indications show that the use of a selection index in which several traits occur could be a promising approach. Such a selection index must be developed for each crop-ecological region combination. In barley for the Syrian region, this could be selection for a dark-green, prostrate growth habit before the middle of February followed by a light green, erect growth habit in March, and heading at the end of March-early April (Van Oosterom & Acevedo, pers. communic.). For other regions in the Mediterranean area, other indices must be developed.

Stability of Resistance to Unidentified Stresses (*biotic as well as abiotic*)

Even if no specific stress factor can be identified, the biomass and yield of a crop vary from year to year and from location to location. These variations in performance must be the collective result of several to many, often unidentified, stress factors. The intensity, duration, and time of occurrence, as well as the identity of these stress factors, must vary from environment (years, locations) to environment. The ranking order of genotypes may vary with the environments, resulting in genotype \times environment (G \times E) interactions.

The cultivars that are most desirable are those that perform in a stable manner at a relatively high level. What are these cultivars and how can they be selected? Because the environments in a certain region vary in their yield levels, it is possible to characterize each environment (one location in one year) by the mean yield of a reasonably large sample of cultivars, the environmental index (E.I.). If a number of cultivars is tested over a series of environments, it is possible to rank the environments according to their E.I. in an order from poor (low yielding) to good (high yielding). Each cultivar to be tested can be compared with the E.I. of each environment. One

can estimate the linear regression coefficient of each cultivar on the E.I. (*Figure 1*), assuming that the deviation from the average reaction to the environmental improvement (regression coefficient = 1.0) is predominantly linear. Two cultivars show a G \times E interaction if the regression coefficients, b , differ. In *Figure 1*, cultivar B is adapted to high yielding environments. It has a b -value larger than 1.0. D is a cultivar adapted to low yielding environments, with a b considerably smaller than 1.0. Cultivars that are widely adapted have a b -value of around 1.0, like B. This is as defined by Finlay and Wilkinson (1963) and Eberhart and Russell (1966), and is valid for the region which the environments represent. The most desirable cultivars, therefore, are those having a b -value of about 1.0 and a high mean yield over all environments.

What is stability in this context? That is less clear. Finlay and Wilkinson (1963) defined stability as little change over environments. In their sense, cultivar D (*Figure 1*) is stable and A highly unstable. The definition is not very useful because such a stability is not really desirable, unless it goes together with a very high mean yield. Cultivars with a very low b -value and yields well above the average do not seem to occur; they have not yet been reported. Eberhart and Russell (1966) gave a quite different and more useful interpretation of stability. Stable cultivars show on average a small deviation from the linear regression line, whereas unstable cultivars have a relatively large deviation. The deviation is expressed as $s^2_{d_i}$. The smaller $s^2_{d_i}$, the better the b -value and the mean, m , over all environments predict the performance in any one environment, provided linear regression describes the G \times E interactions that occur adequately, which is not always the case.

Here again, as with the individual stress factors, it is difficult to define the stability to the undefined complex of stress factors. In this case, it is so difficult because the stability is confounded with the G \times E interaction.

The easiest approach for getting the desirable cultivars is to test promising cultivars over a series of years at a range of locations that represent the growing areas of the crop in the region. This is the best practical way to obtain a series of environments that are representative of the environments the crop may meet in that region. The cultivars chosen are those that have a high yield averaged over all environments tested and that are among the better cultivars in all environments. This ensures broad adaptability, high performance, and a reasonable stability.

If cultivars are tested over years and locations in replicate, it is possible to subdivide the GxE interaction variance in a G x year, a G x location, and a G x year x location interaction variance, whereby the G x location interaction variance often is the smallest, and the G x Y x L interaction variance very considerable. This means that one cannot replace years by locations.

Because of the need for broadly adapted cultivars, it is advisable to start testing at several locations as early as possible in the breeding program. It seems more efficient to have the entries tested at a few to several locations in singular rather than at one location in replicate (Rasmussen & Lambert, 1961; Bhatt *et al.*, 1984).

With the individual abiotic stress factors, it was not possible to separate the stability of resistance from the very large variation in the occurrence of the stress. With the complex of unidentified stress factors, it appears impossible to separate the stability of the resistance from the GxE interaction. Selecting for broad (wide) adaptation through a multi-environment test is the best way at present to obtain cultivars that have a stable resistance to this complex of unidentified stress factors.

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TABLE 1. Winterhardness, cold tolerance, and recovery after freezing periods of 5 winter wheat cultivars in The Netherlands scored on a scale of 1 (very poor) to 10 (very good).*

Cultivar	Winter-hardness	Cold tolerance	Recovery
Capelle Des Prez	3 ₊	3	8
Joss Cambier	5	5	6
Stella	6 ₊	6	9
Manella	8	8	8
Apollo	9	9	9

*Anonymous (1962-1972).

TABLE 2. Homogeneity of occurrence of stress causing factors and ease of assessment (heritability) of the resistance or tolerance to the abiotic stress factor in the field (h^2 -f) or in a greenhouse or laboratory screening test (h^2 -scr).

TRAIT	Homogeneity stress factor in		h^2 -f	h^2 -scr
	Time*	Space*		
Sprouting resistance (wheat, rye, triticale)	3**	8**	5**	5**
Lodging resistance (all cereals)	5	8	7	—***
Resistance to breaking off of the ears (barley)	3	8	5	—
Tolerance to acid soil (barley, wheat)	7	3	5	7
Winterhardness (barley, wheat, triticale)	3	5	4	4
Salt tolerance (barley, wheat)	7	1	2	5
Drought resistance (all cereals)	3	3	1	—
Broad adaptability (all cereals)	3	3	1	—

*In time is within and between seasons; in space is within and between experimental field plots.

**1 = very low; 9 = very high.

***— means no suitable screening test available.

TABLE 3. Root length regrowth (mm) of 10 Brazilian wheat cultivars after the seedlings were grown in a nutrient solution for 72 hours followed by 48 hours in solutions with different Al-concentrations.*

CULTIVAR	Suitable Soils	Al*** concentration in mg/l			
		0	2	6	10
BH 1146	acidic	95	63	40	27
IAC 5	acidic	52	31	23	3
IAC 28	acidic	69	39	31	17
IAC 21	acidic	43	25	19	4
IAC 24	acidic	51	34	29	4
IAC 161	acidic	63	41	10	0
IAC 22	mod. acidic	54	30	13	3
Anahuac 75	slightly acidic	62	0	0	0
IAC 162	non-acidic	66	31	0	0
Paraguay 281	non-acidic	51	12	0	0

*After Camargo & Felicio (1988).

TABLE 4. Grain yield of barley in g/m² on soil of diverse salinity classes in fields varying in levels of salinity.*

Grain yield in g/m ² →	Salinity class in dS/m							
	0-4	4-8	8-12	12-16	16-20	20-24	>24	
	485	431	321	211	102	5	0	
Field very salty Field salty Field not salty	% of field in salinity classes							
	23	26	7	6	11	6	21	
	52	19	10	7	6	1	5	
	100	0	0	0	0	0	0	
Field very salty Field salty Field not salty	% of total yield of the field							Yield g/m ²
	41	41	8	5	4	0	0	
	65	21	8	4	2	0	0	
	100	—	—	—	—	—	—	

*The salinity is measured by measuring the conductivity of soil saturated with water and is expressed in decisiemens/m (dS/m). Seawater diluted to 40% has a dS/m value of about 20. (After Richards, 1983.)

TABLE 5. Expected grain yield in g/m² at 5 levels of salinity and in fields of 3 salinity classes for barley cultivars selected for high yields under non-salty conditions and selected under very salty conditions.

Selected for*	Salinity in dS/m					FIELD		
	0-4	4-8	8-12	12-16	16-20	very salty	salty	not salty
Starting level	485	431	321	211	102	270	387	485
High yielding-1	534	474	353	232	112	297	426	534
High yielding-2	534	470	343	219	100	293	423	534
Very tolerant-1	485	450	390	310	205	297	411	485
Very tolerant-2	460	440	390	315	220	291	397	460

*High yielding-1 represents a cultivar with a yield potential 10% higher than the cultivars on which the experiments were based (starting level). High yielding-2 represents the same yield increase at non-salty conditions, but associated with a slight loss in salt tolerance. Very tolerant-1 represents a highly tolerant cultivar without loss in yield under non-salty conditions, while very tolerant-2 shows a loss of yield potential under non-salty conditions of 5%.

TABLE 6. Yield in tons/ha of 5 barley cultivars in 5 environments (I to V), the regression coefficient, b, of cultivar yields on the environment index, and the mean drought susceptibility index, S.

CULTIVAR	I	II	III	IV	V	II-V Mean	b	S
A	5.0	3.8	3.0	2.2	1.5	2.63	1.13	1.04
B	4.6	3.5	2.7	2.0	1.4	2.40	1.05	1.05
C	4.4	3.5	2.9	2.4	2.0	2.70	0.81	0.85
D	4.2	3.4	2.9	2.4	2.1	2.70	0.71	0.78
E	5.2	4.2	3.6	3.0	2.6	3.34	0.89	0.78
Mean*	4.6	3.5	2.9	2.1	1.6	2.50	1.00	1.00

*Mean over a large number of cultivars. In each environment, this mean represents the environment index.

TABLE 7. Regression coefficient of cultivar yields on environment index (yields averaged over all cultivars per environment), mean yields over 6 environments in tons/ha, yields in the highest (H) and lowest (L) yielding environment,* these yields ln-transformed, the regression coefficients of cultivar yields on environment index after ln-transformation, and the mean drought susceptibility index, S.**

Cultivar or line	Regression coefficient	Mean yield	Yield*		Yields, ln-transformed		Regression coefficient	S
			H	L	H	L		
Anza	1.20	2.67	4.40	0.91	1.48	-0.09	0.86	0.95
Sholeh	1.23	2.56	4.33	0.75	1.47	-0.29	0.97	0.99
Line 14	0.82	1.86	3.04	0.66	1.11	-0.42	0.84	0.93
Line 25	0.82	1.66	2.84	0.46	1.04	-0.78	1.00	1.00
Mean of 7 genotypes	1.00	2.03	3.47	0.56	1.24	-0.58	1.00	1.00

*These yields have been obtained from the mean yields and the regression coefficient because the actual yields were not given in Ehdaie & Waines' publication. As the genotype \times environment interaction was largely of a linear nature, the estimated data presented here must be close to the actual ones.

**Adapted from Ehdaie & Waines (1989).

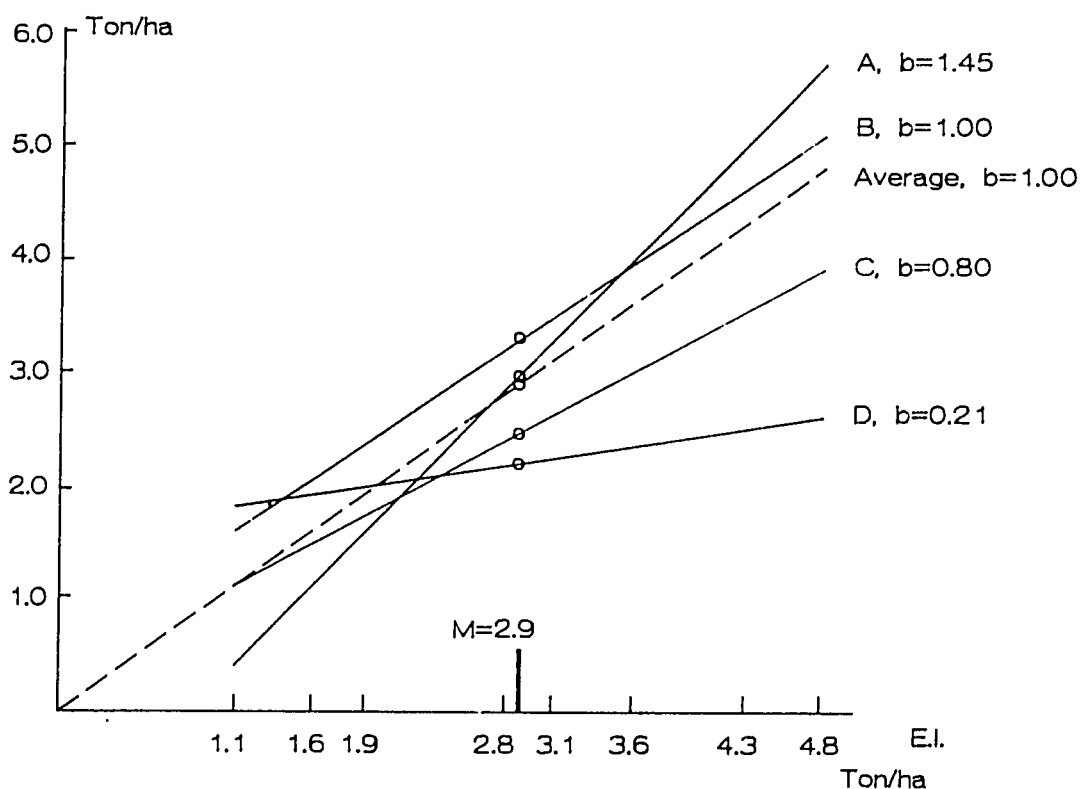


FIGURE 1. Regression of grain yield in tons/ha of four barley cultivars (A-D) on the environmental index (E.I.).*

*The E.I. of each of the eight environments is the average yield over a fairly large number of cultivars in that environment. The average regression of all cultivars on the E.I. has a regression coefficient of $b = 1.0$. The mean yield over all environments is m .

Roles of Abiotic Stress in the Development of Foliar Diseases

Roy D. Wilcoxson*

The title suggests that "environment" is a key factor in the development of foliar diseases of barley as indicated by the equation: Host + Pathogen + Environment = Disease. In referring to this equation, a literal or a mathematical interpretation is not suggested; rather, the equation should be regarded as a tool to organize facts and ideas about plant diseases. In this paper, I shall consider abiotic stress as being induced by changes in the environment that alter disease development, incidence, and/or severity.

I shall not be concerned about those stresses in disease development that might be attributed directly to resistance of barley plants, to virulence of pathogens, or to interactions of pathogens with each other and with other micro-organisms that might be present in the phylloplane of the barley plant. I do this even though I realize that a diseased plant or tissue may be considered a third biological entity, somewhat similar to a lichen, that responds to the physical changes of the environment.

Neither will I consider the stress created by products of microbial interaction that might be on the barley plant surface. Neither are the effects of fertilizers included here because they are not usually applied to foliage. Their effects on the development of foliage diseases of barley may be mediated largely through the agency of the plants as they respond to the fertilizers. Root diseases are probably more directly affected by fertilizers than are foliage diseases.

The components of the abiotic environment to be considered in this paper that may produce stress in the development of barley foliage diseases are the physical factors of the environment, air pollutants, and fungicides.

Temperature and Moisture

Temperature and moisture limit the geographic distribution of barley pathogens and diseases or reduce their importance to certain areas. Temperature and water exert their effects primarily on the growth and development of the pathogens though moisture and temperature have more direct effects on plants that may influence development of diseases.

Support for the above statements may be found in the impressive listing of barley diseases found in the *Compendium of Barley Diseases*, edited by Dr. Don Mathre (1982) and published by the American Phytopathological Society. Let me cite a few examples. For moisture we read: the bacterial stripe blight pathogen is splashed; glume blotch is favored by wet windy weather; spot blotch is most severe during periods of wet weather longer than 16 hours. For temperature we read: teliospores of *Tilletia controversa* germinate best at 5°C but not at 15°C; stem rust development is optimum at 20°C but it is restricted at 15°C; stripe rust development is optimum between 10 and 15°C.

The effects of stress due to excesses or deficiencies of temperature and moisture are often difficult to distinguish in natural environments. As a result, they are often linked, and warm/wet weather diseases or cool/wet weather diseases are frequently mentioned. The following are groupings of barley diseases by weather conditions: warm/wet weather diseases are stem rust, septoria leaf spots, bacterial blight, and spot blotch; cool/wet weather diseases are leaf rust, scald, net blotch, and stripe rust; warm/dry weather diseases are powdery mildew and barley yellow dwarf.

While the above groupings have broad usefulness, they should be used with caution. The terms of reference are imprecise and what one person may regard as cool or warm may be regarded by another in an opposite sense. Furthermore, pathogens function in a range of environmental conditions that makes overlap a distinct possibility. In Minnesota, for example, spot blotch occurs in both the northern and southern parts of the state but epidemics occur only when rainfall is adequate during July and August, the warmest months of the growing season. On the other hand, net blotch occurs only in the northern reaches of Minnesota and epidemics may begin early in the season when moisture is abundant. In Morocco, spot

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blotch and net blotch both occur but net blotch is more common and severe because barley is grown in winter when it is relatively cool and moisture is abundant. As the Moroccan growing season advances, the weather generally becomes warmer and drier, thereby reducing incidence and severity of both diseases.

Temperature

Temperature effects are exerted throughout the life of the pathogens. Temperature affects production, survival, and germination of inoculum as well as the formation of infection structures like germ tubes, appressoria, infection hyphae, and haustoria. Temperature may also affect the development of specific stages of a pathogen as well as the rate of pathogen development.

The minimum, optimum, and maximum temperatures for general development of pathogens or for development of specific stages of a pathogen are called the cardinal temperatures. Knowledge of these temperatures may help explain why diseases and pathogens either fail or succeed in particular environments.

The pathogen is stressed as temperatures rise above or fall below the optimum for growth and development, and eventually it ceases to function. Disease severity and development are reduced as the stress on the pathogen continues, and eventually disease development ceases.

Stripe rust of barley caused by *Puccinia striiformis* may be a useful example of the concept that temperature may restrict development of disease. This disease flourishes at 10-15°C when dew and rain are frequent. It is a well-known cool weather disease. Mycelium survives below -5°C. Cardinal temperatures for the germination of urediniospores are 0, 10-15, and 24°C. Stresses induced by temperatures that are critically above optimum reduce spore germination, pathogen survival and rust development.

In some years, primary centers of stripe rust occur in wheat at Rosemount, Minnesota, when the spring season is cool and wet. However, secondary centers of infection have never developed from the primary infections because summer temperatures are above the optimum for the pathogen. This situation has been observed for many years.

Stripe rust of barley has devastated the crop in certain areas of South America and was recently reported in Mexico. Though it is likely to spread northward into the United States, it is not expected to be a

production problem in Minnesota barley. There are several reasons for this expectation that are related to temperature requirements of the pathogen, as outlined above, and the cultivation of barley in Minnesota. The pathogen is not likely to survive throughout the year in Minnesota because of a lack of suitable host plants during much of the year. There is no alternate host and all of the barley is of the spring type. This means that primary inoculum, blown into Minnesota from southern areas of the United States, will probably arrive during late May or early June and the first cycle of infection may develop because it is usually cool and moist at this time of year. However, secondary cycles of infection are unlikely because the temperatures of late June and early July are too high for germination of the urediniospores. Furthermore, Minnesota's crop is ready for harvest by early August because it is planted early in April.

Whereas temperature induced stresses may affect the growth and development of a pathogen and thereby alter the development of disease, the resistance mechanisms of plants may also be affected. This is probably most clearly illustrated by the Sr 6 gene for resistance to wheat stem rust. Below 24°C, Sr 6 conditions resistance to many isolates of *Puccinia graminis* f.sp. *tritici*, but above 24°C the gene does not function and the plants are susceptible.

Temperature sensitive resistance genes also occur in barley. This was recently noted by Steffenson (1983). Barley genotypes with resistance conditioned by the "T" gene usually produce a mesothetic reaction to *Puccinia graminis* f.sp. *tritici* at 18°C, which makes it difficult to distinguish resistant from susceptible plants. However, at 25°C, uredinia tend to be of the large type, making it possible to recognize susceptible plants.

Treeful (1986) also found temperature sensitive resistance genes in some accessions of *Hordeum spontaneum*, a wild barley of the Mediterranean area. When infected with *Puccinia hordei* at 15°C, some accessions produced small uredinia, indicating resistance. But at 25°C, these accessions produced large uredinia, indicating susceptibility.

While temperature sensitive resistance genes are known, temperature sensitive virulence genes are not. This is probably because studies on the genetics of virulence have been neglected and efforts have been focused to understand the physiological and ecological responses of pathogens to fluctuations in temperature.

Moisture

Water is essential for the development of most pathogens and diseases of barley. The concepts were neatly summarized by Yarwood (1956) into four classes on the basis of the water requirement at critical phases of disease/pathogen development. For diseases caused by viruses and powdery mildew fungi, there is no apparent requirement for water during any of the several stages of disease development, although powdery mildew of barley may be severe during damp seasons. For diseases caused by rust fungi, the principle need for water is during the incubation phase of disease development. For diseases caused by downy mildew fungi, water is required during the incubation and sporulation phases. For diseases caused by bacteria and by some fungi like *Septoria* spp. and *Rhynchosporium secalis*, water is required in all phases of disease development except the infection phase.

Of course, these concepts are an attempt to generalize and we can think of refinements — and perhaps there are some exceptions. However, it seems clear that water stress will be detrimental if applied during the critical incubation and sporulation phases of development for most diseases caused by fungi and bacteria.

For most fungi pathogenic on barley, spores germinate only in water. A few fungi will germinate when relative humidity is between 95 and 99%, but only powdery mildew fungi will germinate below 90% RH. For most of the fungi, mycelial growth across the leaf surface, the formation of penetration structures and penetration requires water and high RH. Once penetration has been achieved, both fungi and bacteria appear to obtain water from the plant tissues to sustain their growth and development as well as to cause disease. However, the severity of some diseases is increased when tissues are water soaked or when infected plants are placed in a saturated atmosphere for several periods of 12 to 24 hours duration.

For powdery mildew or rust fungi, water is not required for production, release, dissemination, or deposition of inoculum. On the other hand, for fungi like *Rhynchosporium secalis* and *Septoria* spp., water is required for reproduction, spore release, dissemination, and deposition. Water is also necessary for development of perfect stages, for spore bearing structures to form, and either moist air or water is necessary for release of ascospores or basidiospores.

Diseases of barley that are caused by bacteria are reduced in incidence and severity if water is not

present. For disease to develop efficiently, plant tissues must be water soaked. Water is also necessary for dissemination and deposition of bacteria and for penetration of plant tissues.

Water may be provided by sprinkler irrigation systems to improve the opportunity for diseases to develop when rain or dew are deficient and the environment is dry. Sprinkler irrigation is used in Minnesota which is located in a transitional zone so far as water is concerned. Some growing seasons in Minnesota may be quite dry at critical periods during development of diseases. At St. Paul, plots are routinely sprinkle irrigated and inoculated with *Bipolaris sorokiniana* to foster development of spot blotch and kernel discoloration. This procedure makes it relatively easy to select for resistance to these diseases and to develop resistant germplasm and cultivars.

The importance of water on disease development will be summarized by a brief review of its importance in the development of scald caused by *Rhynchosporium secalis*. More detail is found in Shaner's (1931) summary of effects of environment on leaf blights.

Sporulation by *R. secalis* continues on wet stubble for more than three months when stubble is alternately wet and dry and at 10-18°C. It also sporulates on necrotic lesions that are wet for about 72 hours and at 10°C. Alternately wet and dry periods tend to reduce sporulation on leaves. Most conidia are splash-dispersed by rain with a few being airborne.

Germ tubes grow at 4-28°C, with 18°C being optimum when leaves are wet. Infection occurs in 24 hours on moist leaves at 18-20°C. Lesions appear within 14 days after inoculation.

Clearly, *R. secalis* requires cool, wet conditions to complete its life processes and to cause disease in barley.

Light

Light includes the ultraviolet, visible, and red portions of the electro-magnetic spectrum. Each component of the spectrum affects the reproductive and growth cycles of both pathogens and plants. While we have considerable information about the effects of light on fungal pathogens, much of this information is derived from controlled laboratory experiments and may not be applicable in the field. In the laboratory, the response of pathogens to light varies with the substrate on which they are grown. However, in the field, pathogens subsist on living plants and plant debris and so the substrate is not

defined except in a biological sense. Furthermore, in the field, effects of light are often confounded with effects of temperature and moisture. Frequently, knowledge about the effects of light on the behavior of a pathogen in the laboratory does not apply in the field.

Despite these comments about the negligible effects of light on plant pathogens and diseases in the field, the effects of ultraviolet irradiation may, in the future, be important. In the press there are frequent references about an increase in ultraviolet irradiation due to destruction of the ozone layer of the atmosphere by air pollutants. We are warned that if this destructive process continues, the earth will be bathed in more ultraviolet irradiation than in the past. It is likely that living organisms of the future will be injured and their physiological processes, including their disease resistance mechanisms, will be adversely affected.

Barley diseases may be affected by ultraviolet irradiation, according to limited studies. The severity of net blotch and of spot blotch increased after plants were exposed to ultraviolet irradiation. Resistant cultivars were rated as susceptible to both diseases after 5-15 minutes of irradiation. Furthermore, irradiation also resulted in barley plants becoming susceptible to *Phoma medicaginis*, a pathogen of alfalfa.

Irradiation of barley with ultraviolet light reduced the severity of powdery mildew regardless of whether the treatment was applied before or after inoculation. Apparently the treatment changed the resistance mechanism of plants and it also killed the mycelium and spores of the pathogen.

Fungicides

Fungicides are a new factor in barley production. It is now possible to seriously consider their use to control diseases of barley because new fungicides have been developed and application techniques have been modernized. As a result, barley seeds and foliage are now treated with protectant and systemic fungicides on a scale that was hardly anticipated 20 years ago.

In Minnesota in some years, thousands of acres have been sprayed with Dithane M45, and in recent years interest in Tilt has greatly increased for the control of spot blotch, net blotch, *Septoria* leaf spots, and leaf rust. This interest will undoubtedly continue and increase now that stem rust is epidemic in barley in the midwestern United States. Seed has also been treated with fungicides to control seedling diseases and loose smut. In Minnesota, as well as elsewhere

in the world, the use of fungicides on seeds and foliage is common. The fungicidal chemicals may be considered to be among the abiotic stress factors that influence the development of foliar diseases.

Protectant fungicides used for seed treatments provide good protection for early infection by fungi causing seedling blight and root rot. However, these chemicals do not provide protection against loose smut. This disease is controlled by carboxin, a systemic fungicide. Failure to control loose smut with fungicides is usually due to the use of the wrong chemical, to the use of inadequate doses of the chemical, or to the non-uniform application to the seeds.

Systemic fungicides applied to seed may persist in plants until after they are in the tillering stage of growth and beyond. Whether these compounds influence the development of foliar diseases depends largely on the concentrations that were applied to the seed and when the foliar disease began to develop. If attempts are made to use systemic fungicides to control foliar diseases, failure is a likely result unless care is taken by the user.

The control of foliar diseases of barley by means of fungicides is not warranted when cultivars are resistant to the target diseases or when environments do not favor disease development. However, these two factors are often ignored when growers are uninformed, when they are greatly concerned about potential disease problems, or when a variety of conditions exist to distract the user and create opportunities for error.

In Minnesota, between 1977 and 1985, the use of Dithane M45 was evaluated on barley to become familiar with its value and to gain experience with potential problems. It was applied at the rate of two pounds of product per acre in 50 gallons of water when plants possessed fully expanded flag leaves, and 7-10 days later. Each year the cultivars Larker, Manker, Morex, and Robust were evaluated at St. Paul, Rosemount, Morris, and Crookston, Minnesota. Diseases of concern were spot blotch, net blotch, leaf rust, and *Septoria* leaf spot.

Dithane M45 reduced the severity of these diseases, but it did not always increase yields. There may be several reasons for this. The procedures usually provided protection for the flag leaf but not for the life of the plant. Sometimes the diseases were not severe enough to produce losses; sometimes diseases developed after the fungicide was no longer effective; sometimes the environment was unusually favorable for disease development.

How successful, then, was the spraying program? With Larker, the cultivar that was susceptible to all of the target diseases, 22 tests were made. Dithane M45 increased yields in nine trials by five or more bushels per acre — enough to be profitable. It increased yields in two trials by four bushels per acre — enough to pay costs. Yields were increased slightly or not at all in 11 trials.

With Manker, Morex, and Robust, cultivars that were resistant to spot blotch but not to the other target diseases, 68 trials were made. Yields were increased enough to be profitable in 12 trials and enough only to pay costs in two trials. Yields were not increased in 54 trials.

The data clearly indicate that fungicide spraying of a barley cultivar that was susceptible to all common diseases in Minnesota was profitable in only about 50% of the trials. On the other hand, spraying cultivars resistant to prevalent diseases was profitable in about 13% of the trials and only in the presence of a disease to which the cultivar was susceptible.

Other reports about the treatment of barley with foliage fungicides have also indicated similar results. Spraying with Mancozeb increased yields of susceptible Larker about 20%, whereas spraying cultivars resistant to spot blotch increased yields only 1 to 10%.

Air Pollutants

Air pollutants are a fact of life in modern agriculture. Today's atmosphere is polluted with various chemicals that were absent or insignificant prior to the development of modern industrial societies. The pollutants are carried into rural areas from production sites in metropolitan centers. During the past 20 years, information has been presented concerning the effects of air pollutants on the development of plant diseases caused by most classes of plant pathogens. Some of this information has been accumulated with the use of barley and wheat as test species.

Enough information is now available to sustain generalizations, although it should be recognized that as more careful studies or additional studies are made, the generalizations may be changed. Much of the information now available on the interactions of pathogens and air pollutants is based on observations or single experiments. Verification is needed and should be based on carefully controlled experiments.

The mechanisms by which air pollutants affect plant pathogens and thereby influence disease devel-

opment have not been closely studied. The pollutants may affect spore germination, growth of germ tubes, formation of infection structures, and mycelial growth and fungal reproduction. The pathogen may be killed along with phylloplane organisms. Furthermore, the structure of the crop canopy may be altered by air pollutants to influence dispersal and deposition of pathogens and vectors and thereby alter the initiation and rate of infection and the course of epidemics.

Sulfur dioxide and ozone are the most important air pollutants, although other pollutants may also be important in specific environments.

The following is a summary of what is known about air pollution effects on plant diseases, especially barley diseases.

No studies have been conducted on the effects of air pollution on barley diseases caused by bacteria. However, information on diseases of alfalfa, corn, kidney bean, and soybean indicate that sulfur dioxide increases the length of latent period, decreases the size of lesions, and reduces disease severity.

No studies have been performed on the effects of air pollutants on diseases of barley caused by viruses. However, air pollutants increase susceptibility to some viruses as noted in bean and corn exposed to sulfur dioxide and infected with southern bean mosaic virus and maize dwarf mosaic virus. Infection with a virus often protects plants from injury by air pollution.

Most studies on the interactions of air pollutants and plant pathogens have been made with fungi and diseases that fungi induce. Studies have been performed with rust diseases of barley, oat, and wheat; with leaf spot diseases of barley; and with root rot wheat. Many studies have been done with crops other than cereal crops. The effects of air pollutants on diseases caused by fungi may vary with plant species as well with cultivars, with the concentration of the pollutants, and the time and duration of exposure. Most studies suggest that exposure to sulfur dioxide and ozone tends to reduce the incidence and severity of rust diseases and powdery mildew, but tends to increase incidence and severity of diseases caused by facultative pathogens like species of *Ascochyta*, *Pyrenophora*, *Bipolaris*, *Fusarium*, *Pseudocercospora*, etc. With these latter diseases, the sites of injury by the pollutants were often the infection courts.

McLeod (1988) studied diseases of Sonja winter barley exposed to sulfur dioxide in the field. The gas was continuously provided, except for short periods,

during winter and spring of 1982 and 1983, at the rate of 0.1222 ppm to 0.440 ppm. The incidence of leaf rust and scald was reduced at all concentrations. The strawbreaker disease increased with concentrations of sulfur dioxide but was less severe at higher concentrations of the gas.

The report of Fehrmann *et al.* (1986) provides food for thought about the importance of air pollutants on cereal diseases. These researchers observed that during recent years in Central Europe, attacks on cereal leaves by pathogenic fungi have become common. Since air pollutants have also become more common in this part of Europe, they theorized that a relationship might exist. Wheat and barley were exposed for six days to sulfur dioxide and ozone prior to inoculation. The severity of infection by *Bipolaris sorokiniana*, *Pyrenophora teres*, *Ascochyta* spp., and *Fusarium nivale* was noted. Exposure to ozone tended to increase severity of each disease, whereas exposure to sulfur dioxide tended to suppress them. Of two cultivars of wheat and barley that were tested, the effects of the pollutants were more severe in one cultivar than in the other.

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Soil-Borne Pathogens as Components of Plant Stress

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Common root rot is the most widespread and destructive root disease of barley and wheat on the Canadian prairies. Other root diseases, such as browning root rot and take-all, occur infrequently and are rarely widespread. However, common root rot occurs wherever barley and wheat are grown.

Common root rot is caused primarily by the fungus *Cochliobolus sativus*, which is better known by the name of its asexual stage as *Helminthosporium sativum* or *Bipolaris sorokiniana*. Several species of *Fusarium* also can be involved, but usually are considered of minor importance in western Canada.

Common root rot is characterized by a brown discoloration of the roots, subcrown internodes and the base of the culm. This disease often goes unnoticed because of an absence of aboveground symptoms and can be detected only by examining the roots and subcrown internodes. However, during periods of moisture stress, symptoms such as stunting of the plant and yellowing of the leaves often are evident. Usually, diseased plants are scattered throughout the field.

Cochliobolus sativus can attack all parts of the barley plant. It causes the formation of brown lesions on the leaves, a symptom known as spot blotch. It also infects developing kernels, causing a black discoloration at the germ end of the seed known as black point. Infected seed is an important factor in stand reduction caused by seedling blight. However, in western Canada, this fungus is a major concern as the cause of common root rot or crown rot in barley and wheat. The most recent root rot survey (Piensing *et al.*, 1976) reported that this disease was responsible for annual yield losses in barley averaging 10.3%. In wheat, common root rot reduces yield on average by 5 to 6% (Ledingham *et al.*, 1973). These reductions in yield were primarily due to lower tiller numbers in barley; in wheat, the number of kernels per spike and kernel weight also were reduced.

In the absence of a susceptible host, *C. sativus* survives as thick-walled conidia in the soil or as conidia and mycelia in infected crop debris. Conidia can remain viable in the soil for two to three years in the absence of a susceptible host species. Root

exudates from susceptible hosts trigger germination of the conidia, ultimately resulting in infection of the roots and subcrown internode. The fungus sporulates on infected tissue as it becomes necrotic.

Disease severity ratings are based on the amount of discoloration occurring on the subcrown internode. Plants are grouped into one of four different categories and a weighted analysis is used to convert these values to a percentage root rot rating. These percentage values generally correlate with the amount of root discoloration caused by the pathogen but do not always closely agree with the amount of yield reduction. This method of disease assessment provides a rapid means for the evaluation of different cultivars or lines for resistance. The development of resistant cultivars of wheat and barley has been effective in reducing losses caused by common root rot in both barley and wheat. No cultivars have been developed that possess complete resistance to the root rot fungi. Instead, most barley and wheat cultivars carry a level of resistance that ranges from moderately susceptible to moderately resistant. There have been several reports of differences in host range between *C. sativus* isolates. However, races differing in their ability to cause disease on different cultivars have not been reported and root rot resistance in barley and wheat is a stable trait. Environmental factors can influence the amount of disease at different locations, but generally the ranking of different cultivars for root rot severity remains fairly constant between locations.

Barley cultivars differ in their ability to recover from root damage caused by *C. sativus*. Several studies have demonstrated that cultivars with similar levels of root rot severity can differ in yield loss. Yield loss determinations are based on comparisons of the yields of healthy plants with those of diseased plants from the same plots. Certain cultivars are able to recover from early injury that reduced tiller number and are able to produce either more kernels per

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spike or heavier kernel weights, especially if soil moisture conditions become more favorable. Such cultivars are considered to be root rot-tolerant because their yields are not greatly reduced by the disease.

Rotation with noncereal crops or summer fallowing for two or three years is recommended for reducing yield losses caused by common root rot. Studies on the influence of different crop species on soil inoculum levels have shown that spore numbers tend to be highest under either barley or wheat (Chinn, 1976). Under nonhost crops, such as rye and oats, the number of conidia in the soil is less than under barley or wheat but is still sufficient to result in high root rot severity in subsequent crops of wheat or barley. A recent study by Duczek *et al.* (1985) demonstrated that only a low number of conidia in the soil is needed to reach the threshold required for high disease severity in barley and wheat.

On the Canadian prairies, the majority of dryland acreage is used for the cultivation of wheat or barley. This makes it difficult for producers to establish long-term rotations with crops other than wheat or barley.

Isolates of *C. sativus* differ in their ability to infect the leaves of different grass species (Kline & Nelson, 1971). Wood (1962) also reported that isolates of *C. sativus* differed in their ability to cause seedling blight on different cereals. This suggests that isolates of *C. sativus* might also differ in their ability to cause root rot in wheat and barley.

A study was initiated to examine the effect of cropping history on root rot severity in barley and wheat (Conner & Atkinson, 1989). The research was conducted using soil from different field sites on the Lethbridge Research Station. At the wheat site, a susceptible wheat cultivar had been grown for five consecutive years. At the barley site, a susceptible barley cultivar had been grown on the land for the same length of time. A disease-free site that had been cropped to noncereal crops for five years also was used. Soil from each site was used in greenhouse tests to determine if previous cropping history had an effect on the relative amount of root rot in resistant and susceptible wheat and barley cultivars. The results of this study demonstrated that soil continuously cropped to wheat produced significantly more disease on wheat than on barley. Conversely, soil continuously cropped to barley produced significantly more root rot on barley than on wheat. Differences in root rot resistance among wheat and barley cultivars were apparent and consistent on both wheat and barley soil. However, differences in root rot

resistance were most apparent among barley cultivars on barley soil and among wheat cultivars on wheat soil.

Field tests were conducted at the wheat and barley field sites in 1987 and 1988. At these test sites, the wheat cultivars tested included the susceptible Cypress, the moderately susceptible cultivar Leader, and the moderately resistant cultivar Canuck. Barley cultivars included the susceptible Galt and moderately resistant Bonanza and Klages. These cultivars were planted in replicated trials at each location. The 8-row plots were divided in half, using 4 rows for yield and 4 rows for evaluating root rot severity. Root rot severity in each plot was evaluated at anthesis, the mid-dough stage, and at maturity. The results from the field agreed with those from the greenhouse study. The effect of cropping history on differences in root rot severity in wheat and barley was apparent at each sampling date. Root rot always was most severe in the crop that had been grown previously at the site. These differences were consistent in each year of the study.

However, the differences in root rot severity could not be related directly to differences in yield. The effect of reduced root rot development on the relative yields of the different barley and wheat cultivars was not clear. This was at least partially due to inherent differences in the yield potential of the cultivars in the absence of disease. Differences in root rot tolerance might have further confounded the effect of root rot on yield. These tests are being repeated using lines and cultivars with similar genetic backgrounds but differing in root rot resistance.

Comparisons of isolates of *C. sativus* from the wheat and barley fields showed that an isolate from the wheat field caused the most severe disease development on wheat, whereas an isolate from the barley soil caused the most severe root rot on barley. This agrees with the findings of a recent study by El-Nashaar and Stack (1989), who compared the aggressiveness of *C. sativus* isolates from a root rot nursery in North Dakota where wheat had been grown continuously for more than 100 years, and isolates from commercial fields where wheat was grown in rotation. They found that the isolates from the root rot nursery usually caused more disease on wheat than did isolates from commercial fields.

These results suggest that continuous cropping to wheat or barley results in selection of isolates that are more virulent on that particular crop species. This shift in virulence likely is caused by an increase in the frequency of isolates that are highly virulent on

the crop species. *Cochliobolus sativus* is known to be a heterokaryotic fungi, so it may be that continuous cropping of either wheat or barley results in the selection of isolates with a higher frequency of nuclei carrying the genes for virulence on that particular crop species. These results also suggest that virulence on wheat and barley is controlled by different genetic factors. Research is currently underway to examine the genetics of virulence of *C. sativus* on wheat and barley.

Long-term rotation studies have been established to determine the length of time required for a shift to increased virulence on either wheat or barley. The benefits of reduced root rot severity associated with improved crop rotation will be assessed using more genetically uniform lines with similar yield potentials but which differ for root rot resistance. New recommendations for better rotation systems that limit root rot severity will be based on these studies.

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The Role of Stress on Plant and Insect Interactions

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Introduction

Outbreaks of pestiferous insects have plagued humans throughout history. From mankind's point of view, an outbreak is "an increase in the population of an organism that has a deleterious influence on human survival and well being" (Berryman, 1987). Insects have and continue to destroy man's crops in the field and in storage, and vector pathogens that debilitate and decimate human populations.

Berryman (1987) has reviewed the various hypotheses formulated by different authors to explain the causes of insect outbreaks. These hypotheses are summarized as follows:

- ▶ Outbreaks are caused by dramatic changes in the physical environment such as sun spots.
- ▶ Outbreaks are caused by changes in intrinsic genetic or physiological properties of individual organisms in the population.
- ▶ Outbreaks are due to trophic interactions between plants and herbivorous insects, or prey and predators.
- ▶ Herbivorous insect outbreaks are due to qualitative or quantitative changes in host plants that are usually caused by environmental stresses.
- ▶ Outbreaks result when pest populations escape from the regulatory influence of their natural enemies.
- ▶ Outbreaks occur when pest populations cooperatively overwhelm the defensive systems of their hosts.

I will discuss here the induction of herbivorous insect outbreaks resulting from environmental stresses that cause qualitative and quantitative changes in host plants. These stresses may be biotic or abiotic factors and affect the pest insects directly through host plant quality and quantity and through trophic interactions between host plants and pest insects and their natural enemies.

The types of biotic and abiotic stresses to which a plant may be subjected are illustrated in *Figure 1*. The various stresses to be discussed are: the biotic

stresses, including insects and pathogens; and the abiotic stresses, including soil minerals, water, temperature, light, pesticides and growth regulators, air pollution, and mechanical damage.

Environmental stresses have a number of different effects on plants which determine the suitability of the plants as hosts for insects. Among these are plant growth and development, morphology, texture, color, temperature, nutritional quality, and allelochemical content (Mattson & Haack, 1987). These host plant factors influence populations of herbivorous insects through their effect on insect behavior and insect physiology, and by their trophic level effects on parasitoids and predators. The host plant qualities affect the rate of colonization of a crop within an agroecosystem through host location, host recognition, host acceptance, and host suitability (Ferro, 1987). Host suitability is partially dependent on the biochemical composition of the plant, and thus the nutritional value of the plant to herbivorous insects. Plant nutritional factors affected by the various stresses are the balance of carbohydrates, nitrogen and amino acids, water content, minerals and salts, vitamins and sterols, and secondary metabolites (Riemer & Whittaker, 1989).

Global Importance of Plant Stress

Agricultural productivity is determined by a complex of interactions of plants with their abiotic and biotic environment. Climate is a major abiotic factor determining the crops that can be grown in an area and their productivity. The cool, damp weather that contributed to the Irish potato famine in the 1890s is a model example of a climate-related food disaster (Schneider & Bach, 1981). Of Ireland's initial population of six million people, two million died and two million emigrated. In the last two decades, unfavorable weather patterns have had severe impacts on

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global food production. Indeed, droughts, floods, and extreme temperatures have been a major constraint on crop production in the U.S.A. during this current crop season.

The most severe biotic outbreak the fragile earth has encountered is the phenomenal increase in the human population. As world population has continued to increase, there has been intensified pressure on the little remaining cropland, especially in developing countries. From 1950 to 1975, the world population increased at a more rapid pace than did the opening of new land to cultivation, with a resultant decrease in per capita area in cereal crops from 0.241 to 0.184 (Brown, 1981). Much of the world's land is not suitable for cultivation. In spite of the low percentage of existing good cropland, we are losing cropland at an alarming rate. The current rate of cropland loss on a world basis is unprecedented and affects all countries of the world — both rich and poor.

Loss in cropland productivity has resulted from high populations that have put in motion a combination of economic, social, and ecological forces causing soil mineral depletion, soil erosion, desertification and waterlogging, and salinization of irrigated land. More than 100 tons of top soil per hectare are lost to erosion as tropical hillsides are brought under cultivation (Slater, 1981). Desertification is progressing at the rate of six million hectares per year (Hekstra, 1981). Irrigated areas of the United States that were once lush are becoming unproductive. In the western states, water is being diverted from crop irrigation to assuage the thirst of the rapidly expanding cities. Pump irrigation in some areas is causing the water table to drop faster than it can be replenished. It is evident that inadequate water and soil management are severely altering the quality of soil over vast areas of the world. Plants growing in these areas are stressed by the adverse soil conditions and suboptimal water quantities. In addition, other physicochemical stresses of human origin, such as air pollution, and subsequent acid rain, pesticides, global warming, and ozone layer depletion, are playing major roles in plant growth and quality and significantly affect plant-insect interactions.

Plant Stress-Insect Interactions

All plants are dependent on their environment for growth and development. "Environment includes all of the factors and forces prevailing internally and externally on, around, and in the plant" (Treshow,

1970). Biologists use the term "stress" for "any environmental factor potentially unfavorable to living organisms" (Levitt, 1972). In this section, we consider stress as "any abiotic or biotic factor of the environment that affects plant physiology, chemistry, growth, and/or development in such a way that plants perform below the average for a region" (Heinrichs, 1988). Some of the major environmental stresses and their plant-mediated effects on herbivorous insects are discussed in the following subsections.

Soil Minerals

Along with water and temperature stress, mineral deficiencies and excesses occur throughout the world and are among the most important constraints to crop production (Christiansen, 1979). Each plant requires a specific, optimal amount of the essential elements and the ratio between the elements is vital. Of the 17 essential elements, 6 are used in large quantities and are thus referred to as macronutrients (nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur). Essential elements used by plants in small amounts are referred to as micronutrients (iron, manganese, boron, molybdenum, copper, zinc, chlorine, and cobalt). The plant-mediated effects of three macronutrients — nitrogen, phosphorus, and potassium — on insects are discussed in this subsection. Little has been published on the plant-mediated effects of micronutrients on insects.

Nitrogen is the most limiting element in soil because of low nitrogen in parent materials and because it is easily lost through leaching and evaporation. Nitrogen is particularly important to insects and mites as there exists a significant difference between the nitrogen content of plants (about 2%) and insects (reaching up to 7%). For an insect to grow, it must locate the source of high nitrogen in a plant and consume a sufficient amount.

The effect of nitrogen fertilization on insect incidence varies depending on the insect species, host plant species, soil fertility in regard to nitrogen and other elements, and possibly other environmental factors (Dale, 1988). In 23 studies including nine crops in India, nitrogen fertilization increased insect incidence in 17 trials, decreased incidence in one, and had no effect in five trials (Singh & Agarwal, 1983). Increased rates of nitrogen fertilization increase amino acid and amide levels and make the plant more succulent by increasing tissue softness and by increasing the water content. The increased rates also help plants to compensate for damaged parts, to rapidly pass critical development stages, and to escape insect attack (Jones, 1976).

Second to nitrogen, phosphorus is the most limiting element in soils. A lack of phosphorus prevents other nutrients from being acquired by plants (Brady, 1974). Plants deficient in phosphorus are often dark green in color and maturity is delayed. The few published reports indicate that plant-mediated effects of phosphorus on insects are minor.

Plants need large amounts of potassium. A low potassium supply frequently favors the development of insects and mites, whereas optimum or high potassium has a depressant or neutral effect (Dale, 1988). A possible reason for the reduction of pests by increased potassium may be due to a higher proteogenesis in plants, and thus a subsequent elimination of amino acids and reducing sugars in the sap, both of which are favorable for the reproduction of sucking insects.

Ratios of the major elements in plants are important factors in plant suitability for insects. High nitrogen and high N/K ratios often stimulate insects and mites (Perrenoud, 1976). Thus, increasing nitrogen should be balanced with potassium. Plots receiving a balanced fertilizer treatment are better able to withstand herbivory and recover from injury faster.

Phenological changes due to mineral fertilization can alter the degree of damage by insects to crop plants. Soil application of NPK decreased frit fly (*Oscinosoma pusilla* Meig.) damage to barley by increasing the tillering rate of lateral stems. Injury to barley seedlings is most severe when the main stems are attacked. Injury to lateral stems lowers yields much less. Barley grew rapidly after fertilizer was added to the soil, and the frit fly preferentially attacked the lateral stems; in the control plants, flies mostly attacked the main stem, with consequent greater yield losses (Gurevich *et al.*, 1971).

Insect Responses to Mineral-Stressed Plants

The level and type of effects of plant-mediated mineral stress on insect populations vary significantly, as many interacting factors are involved. Some of the most common and general effects are discussed below.

Food preference. Prestidge (1982) reported that the occurrence of a certain insect species on a given plant is related to the nitrogen level of the host plant. Some species switch host plants or switch from one part of the plant to another when nitrogen concentrations change.

Consumption and digestion of food plants. Insects often consume more food to compensate for the low quality of host plants on which they live

(Slansky & Scriber, 1985). The digestive capacity of insects seems to increase with the nitrogen level of their food (Scriber, 1984). Insects feeding on nitrogen-rich foods, such as phloem sap and pollen, have relatively high digestibility values compared to those feeding on nutrient-poor plant parts.

Insect growth and development. The size of insects, duration of larval instars and the growth efficiency are affected by the nutritional value of the host plant. Larvae of the cinnabar moth reared on fertilized plants produced larger pupae than those on unfertilized plants (Dale, 1988). Body size affects survivorship and fecundity which can contribute to outbreaks. Usually larval development is inversely related to nitrogen level of the host plant (Al-Zubaidi & Capinera, 1984). Prestidge (1982), however, showed that high levels of nitrogen in the food lengthened instar duration of some leafhoppers feeding on *Holcus lanatus*.

Poor quality or inadequate food increases herbivore developmental time and decreases fecundity. Increased developmental time increases exposure time to predation which, when combined with decreased fecundity, may significantly slow herbivore population growth rates (Gutierrez, 1986).

Fecundity and oviposition. Insect fecundity is generally related to the nutritional quality of the host plant on which an insect feeds. Fennah (1969) reported a positive correlation between leafhopper fecundity and host plant soluble nitrogen levels. The host plant quality of larval detoliators influences egg production of their imagines. Brewer *et al.* (1985) reported that the number and weight of eggs laid by the western spruce budworm (*Choristoneura occidentalis* Freeman) were highest when larvae fed on foliage from trees grown at the mid-range nitrogen level.

Population growth. In agroecosystems, application of nitrogenous fertilizers within an optimum range may lead to a corresponding increase in insect populations as the fertilizer amount is increased. But nitrogen above or below this range may often be detrimental (Jansson & Smilowitz, 1986). Weight, feeding rate, and population growth of the rice brown planthopper (*Nilaparvata lugens* Stål) (Figure 2), increased with increasing levels of nitrogen fertilizer on both *N. lugens* susceptible and resistant rice varieties (Heinrichs & Medrano, 1985). Cheng and Pathak (1972) linked fecundity levels and consequent population increases of rice leafhoppers to the content of asparagine, an amino acid constituent of the amide fraction in rice plants. A table listing the effect of

fertilizer on the population of various insect species on different plant species is given in Dale (1988).

Wing morphism. Changes in the amino-N balance and in the concentration of amino acids, amides, and salts — all of which are liable to change according to the nutrient status of soils on which plants grow — are known to affect the wing form of sap-feeding insects. Evans (1938) demonstrated a negative relationship between the number of alate insects and the protein nitrogen content of plants. Fertilization leads to superior host plant nutritional quality that has a brachypterizing effect on planthoppers. Stressed or senescing host plants may trigger macroptery in insects, as is the case of *N. lugens* females on wilted rice plants (Dale, 1988).

Sources of Variation in Effects

There is a great deal of variation in the effects on insects caused by soil nutrient changes that are transmitted through host plants. Among these are soil and insect factors.

Among soil factors are the sources, forms, and availability of nitrogen, and soil pH. Plants growing on nitrate or ammonium show differences in their chemical constitution. Plants grown on ammonium usually accumulate amino acids and amides and contain much lower levels of organic acids than nitrate grown plants (Kirkby, 1968). Moore and Clements (1984) have shown that the form of nitrogen source may change plant-mediated effects on insects such as herbivore phenology and species composition. Perennial ryegrass plots receiving nitrogen as ammonium sulfate contained more stem-boring dipterous larvae than those that received a calcium treatment. Acidic soils affect the nutritional quality of plants by inhibiting nitrifying bacteria, and nodulation and minerals such as phosphorus become largely unavailable (Buckman & Brady, 1969).

Intraspecific variation in insects may be a reason for discrepancies in studies on plant stress-insect interactions. Biotypes respond differently on the same host. For example, the four biotypes of the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), had different body weights when reared on Reno barley (Singh & Painter, 1964). Biotypes may have different nutritional requirements and thus respond differently to plant-mediated mineral stresses. Even males and females of the same species may respond differently, as indicated by studies on the spruce budworm in Douglas fir trees with different concentrations of foliar chemicals (Redak & Cates, 1984).

Water

Both water excess and deficit alter insect-plant relationships in a myriad of interacting, dynamic ways. "Water stress" usually refers to a deficit, rather than an excess (Levitt, 1972). There is little literature on the subject of the plant-moderated effects of flooding on herbivorous insects. Therefore, only water deficit effects will be discussed.

Numerous reviews have covered the subject of drought stress (Kozlowski, 1972; Levitt, 1972, 1960). Moisture stress affects several plant processes, and stress directed alteration of the chemical and physical composition of plant tissues also alters the quality of plants as food for insects. Moisture deficits cause morphological and physiological changes in plants (Parsons, 1982). Morphological responses to water deficits consist of leaf shedding, leaf rolling, leaf angle changes, and an increase in the root-to-shoot ratio. Physiological changes include leaf cuticular wax thickness, transpiration, respiration, stomatal behavior, photosynthesis, translocation, mineral nutrition, and protein breakdown (Parsons, 1982; Treshow, 1970). These factors affect insects by altering their microenvironment, and by altering such characteristics as the toughness and nutritional value of their food and the effectiveness of the plant's defense (Holtzer *et al.*, 1988). Increases in plant metabolites may affect insects at the nutritional-physiological level, or they may alter behavioral responses such as attraction to plants, length of time spent feeding, and preference for specific plants or locations on plants (Bernays & Chapman, 1978). In the following subsections, we discuss the plant-mediated effects of moisture deficits on insect nutrients, defensive chemicals, and plant growth regulators, and on the microenvironment of herbivores.

Insect Nutrients

Availability of organic nitrogen (protein, amino acids, and related compounds) is often a limiting factor in the population growth of insect herbivores (Scriber, 1984). Nitrogen metabolism is an integral part of insect growth, development, and reproduction and is among the plant processes most sensitive to water deficits. In addition to nutritional effects, nitrogen availability is important at the behavioral level. The preference of grasshoppers for water-stressed plants was reported to be related to the phagostimulatory effect of increased levels of proline and valine (Haglund, 1980).

Water stress has important effects on carbohydrate metabolism in plants. However, there is little evidence that effects of water stress on carbohydrate availability play a direct role in insect population growth. On the other hand, the indirect role of changes in plant carbohydrate metabolism induced by water stress may be substantial. For example, nitrogen metabolism is clearly tied to carbohydrate metabolism, as is the size and quality of fruit and seeds (Kramer, 1983). As a result, quality of available food may be enhanced for some insect herbivores because of an increased concentration of nitrogen, while the quantity of food available to the same or other herbivores is reduced (Hanson & Hitz, 1983).

Water content of leaves limits insect growth through its direct nutritional role and through feeding preference. The grasshopper, *Melanoplus differentialis* (Thomas), preferred to feed on and performed better on wilted sunflower (Lewis, 1984).

Defensive Chemicals

A variety of secondary metabolites functions in the chemical defense of plants against insect herbivores. Among these are toxic amino acids, cyanogenic glycosides, alkaloids, flavonoids, and others that are affected by water stress. Plant defensive chemicals can be toxic to insects, or they can reduce the plant's digestibility (Rhoades & Cates, 1976). Interactions between some defensive chemicals and nutrients can make nutrients unavailable, even if they are present in large quantities (Reese, 1981). In addition to direct effects on herbivores, defensive chemicals have been shown to play a role in the effectiveness of natural enemies (Price, 1986).

Plant Growth Regulators

There is evidence that the plant growth regulators (abscisic acid, indoleacetic acid, cytokinins, ethylene, and gibberellins) respond to plant water stress (Kramer, 1983). Grasshoppers have been shown to respond to plant growth regulators (Visscher-Neumann, 1982). Depending on the growth regulator, increased concentration either increased or decreased longevity and reproduction.

Microenvironment of Insect Herbivores

The water stress experienced by a host plant can have a significant impact on the microenvironment experienced by herbivores. Long-term water stress can produce permanent changes in canopy structure, whereas transient water stress affects leaf temperature and humidity through changes in

stomatal behavior. Microenvironmental changes may affect the behavior and physiology of the host insect (Holtzer *et al.*, 1988).

Temperature

Temperature is one of the most important environmental factors affecting the physiological and behavioral interactions of insects and plants. However, the study of how temperature-induced stress affects host plant suitability for insect herbivores is plagued with the difficult task of separating temperature effects from free moisture and humidity effects (Benedict & Hatfield, 1988).

Tingey and Singh (1980) proposed mechanisms whereby temperature induces changes in host plant suitability to insect herbivores:

- ▶ Temperature-induced stress causes changes in plant physiology that affect the expression of genetic resistance, resulting in changes in the level of allelochemical and/or morphological defenses and/or nutritional quality of the host. Insects feeding on temperature-stressed plants have altered growth, development, reproduction, mineral and/or behavior.
- ▶ Temperature-induced stress can directly affect plant physiology resulting in altered plant growth and development and thus affect plant response to insect injury (increased or decreased tolerance).
- ▶ Temperature-induced stress can directly affect insect behavior and physiology.

These three mechanisms are factors that increase or decrease, directly or indirectly, herbivore capability to utilize a food resource. The effects of temperature-induced stress on plant nutrition and chemical defenses, plant morphology, and plant tolerance to insect injury are discussed next.

Plant Nutrition and Chemical Defenses

Both low and high temperature affect primary and secondary plant metabolites. Decrease in ATP at low temperatures leads to an increase in the carbohydrate and amino acid levels due to a lack of energy available for the conversion of these compounds to secondary products (Graham & Patterson, 1982). Changes in the biosynthesis of secondary products such as phenolics can have an impact on the suitability of plants as hosts for insects.

High temperatures cause severe metabolic disruptions affecting the plant, but it is difficult to

separate the effects of high temperatures from drought stress. Protein denaturation can affect proteins and lipids that are associated with the cell membrane and involved with synthesis of allomones and kairomones (Benedict & Hatfield, 1988). In general, there is a diversity of responses of secondary compounds to high temperatures and there tend to be increases in the plant products associated with these secondary metabolites.

Plant Morphology

Temperature-induced plant stress can cause changes in the leaf surface that results in a less desirable forage for phytophagous insects. This stress also can induce morphological responses, such as leaf rolling or wilting, that cause a change in the microclimate within the canopy. Even small temperature changes of less than 3°C can be expected to have an impact on insect population dynamics (Benedict & Hatfield, 1988).

Plant Tolerance to Insect Injury

Although there is little experimental evidence, it is expected that certain plant species can better tolerate insect damage within a particular temperature range than other species (Tingey & Singh, 1980). Sosa and Foster (1976) found that host plant suitability and/or the virulence of the Hessian fly on wheat increased at higher temperatures. Increased tiller production of some wheat cultivars at high temperatures was suggested as a form of tolerance that affects the yield loss caused by a decrease in the level of antibiosis and/or non-preference to the Hessian fly.

Temperature-Induced Plant Stress-Insect Interactions

Most examples of temperature-induced host plant suitability changes appear to result from changes in levels of allelochemical or nutritional quality of the host plant. Evidence as to exactly how these changes affect insects is lacking. As Tingey and Singh (1980) have suggested, the interactions between temperature, pest biology, plant physiology, and other environmental factors are complex. Most examples of the effects of temperature-induced plant stress on insects are for cool season aphids. Information on other insects is limited.

Dahms and Painter (1940) were perhaps the first to report on the effect of temperature on the level of insect resistance in host plants. They found that when field temperatures decreased from 16° to 7°C,

resistance of alfalfa plants to pea aphid population growth was lost. Isaak *et al.* (1963) later reported similar results for the pea aphid and spotted alfalfa aphid. They concluded that the expression of some unknown aphid resistance factor(s) in the resistant clones is modified by temperatures. This may be due to improved nutritional quality as a result of the accumulation of amino acids and carbohydrates, at the expense of allelochemicals, when plants are exposed to cool temperatures.

The level of resistance of sorghum to the greenbug decreased as temperature decreased from 32° to 10°C (Schweissing & Wilde, 1979). Tolerance to greenbug biotype C, however, increased in susceptible sorghum as temperature decreased. In contrast to sorghum, greenbug resistance in barley, oats, and rye was not altered by decreasing temperature (Schweissing & Wilde, 1978).

Wheat having genes for resistance was observed to lose the expression of resistance to the Hessian fly as temperature increased (Cartwright *et al.*, 1946). Sosa and Foster (1976) confirmed the report of Cartwright *et al.* (1946) that wheat lines with different genes for Hessian fly resistance responded differently to insect attack at high than at low temperatures. When the resistant wheat lines were infested by Hessian fly races B, C, D, and Great Plains, the cultivars had different tillering rates and populations of the Hessian fly, depending on the fly race, wheat cultivar, and constant temperature used. As in other studies, the authors did not prove whether temperature-induced changes in the host plant and/or the Hessian fly resulted in a change in level of host plant suitability.

Light

The electromagnetic spectrum ranges from 0.0001 nm for gamma rays to 10^{15} nm for AC power (Berenbaum, 1988). Visible light is in the 390-780 nm range and ultraviolet light is 286-390 nm. The range of wavelengths that is ecologically important to plants is in the violet and red range of 400 to 450 nm and 600 to 700 nm, respectively, and these wavelengths are known as photosynthetically active radiation.

Photosynthetic efficiency determines the rate of photosynthate accumulation and affects the suitability of plant tissues as food for insects. Shading reduces photosynthesis and may increase the susceptibility of a plant to insect attack. Resistance of wheat to the wheat stem sawfly (*Cephus cinctus* Norton) is related to the degree of stem solidness which, in turn, is

correlated to the amount of seasonal sunshine (Berenbaum, 1988). Photosynthetic rate is also believed to affect the suitability of plants as hosts for insects through the production of allelochemicals, as indicated in Table 1.

The absence of UV light affects the allelochemical content of plants. The decreased flavonoid content of greenhouse-grown vegetables may render them vulnerable to aphids, whiteflies, and other greenhouse pests. UV light also affects the qualitative composition as well as the quantity of allelochemicals. The wild parsnip, *Pastinaca sativa* L., produces at least six different furanocoumarins — chemicals with behavioral and toxicological effects on herbivorous insects. When wild parsnips are grown in the absence of UV, the absolute amounts and the relative concentrations of the furanocoumarins change (Zangerl & Berenbaum, 1987). UV also has qualitative effects on plant chemistry. Phototoxins, chemicals that are toxic to insects, are produced through the process of photoactivation which is influenced by the degree of UV light (Berenbaum, 1988). Depletion of the ozone layer has potential for increasing the amount of UV light and thus changing the suitability of plants as hosts for insects.

Pesticides and Plant Growth Regulators (PGRs)

Insecticides, herbicides, and plant growth regulators used to manipulate agricultural systems have direct and indirect effects on insects which influence population levels. They also have plant-mediated effects which are of major importance in regulating insect populations. These include phytochemical, physical, and morphological changes that alter the plant's suitability as a host for insects.

Insecticides

Insecticides can affect insect populations through direct or plant-mediated indirect effects. The direct effect of insecticides is rate dependent. High rates are toxic and kill insects, and sublethal rates are stimulatory resulting in an increase in reproductive rate, a phenomenon termed "hormoligosis" (Luckey, 1968). Insecticides also have been shown to change the chemistry of plants. Insecticide-induced resurgence of the brown planthopper, *N. lugens*, in rice in Southeast Asia has been attributed to a complex of direct and plant-mediated effects plus the effect on natural enemies (Heinrichs & Mochida, 1984; Reissig *et al.*, 1982a, 1982b; Chelliah & Heinrichs, 1980; Chelliah *et al.*, 1980). Brown planthoppers on

insecticide-treated plants have a high feeding rate, greater fecundity, shorter nymphal duration, and higher adult longevity than hoppers feeding on control plants. It is difficult to determine the extent of direct effects of the sublethal insecticide doses on the insect and the extent of plant-mediated effects. Venugopal and Litsinger (1983) found that carbofuran, an insecticide which induces resurgence of the brown planthopper, causes changes in rice plant chemistry. Increases in populations of the rice blue leafhopper (*Zygina maculifrons* Mott.) have been attributed to the low calcium and carbohydrate levels and increased nitrogen concentrations in plants treated with systemic insecticides (Mani & Jayaraj, 1976). They suggested that the reduction of calcium and carbohydrates and the increase of nitrogen caused a weakening of the cell wall, allowing easier stylet insertion by the probing leafhoppers.

The changes in insects and plants exposed to insecticides can result in a pest that is biologically predisposed to inflict greater than normal injury to its host plant, a host plant that is more favorable to the pest, or a combination of the two phenomena (Riley, 1988). There is currently a dearth of literature on the basic mechanisms involved in plant-mediated effects of insecticides on insects. However, through an understanding of how plant-insecticide interactions influence arthropod communities dependent or affected host plants, and the development of the methodology to quantify these effects, a clearer picture will emerge as to how host plant quality affects the status of insect pests and non-target natural enemies.

Herbicides

Campbell (1988) conducted an in-depth review of the plant-mediated effects of herbicides and growth regulators on insects. Because of the obvious modifications herbicides and plant growth regulators induce in normal plant metabolism, a majority of their effects on insect populations are due to changes in the quality of host plants as a source of food. However, the biochemical mode of action is often unclear. In addition to changes in food quality, changes in the physical structure of the plant have an impact on the plant as a source of refuge or as an oviposition site for insects.

The herbicide 2,4-D has received the most attention. Maxwell and Harwood (1958) reported that treatment of broad beans with 2,4-D increased pea aphid populations. They suggested that the increased aphid reproduction on treated plants was

due to higher free amino acid levels. MCPA applied to barley in a 0.16% solution caused an increase in English grain aphids, greenbugs, and oat bird cherry aphids by 2, 34, and 29%, respectively (Hintz & Schulz, 1969).

Increases of stem boring insects, such as rice stem borers and European corn borers, on phenoxy-herbicide treated plants have also been reported (Ishii & Hirano, 1963; Oka & Pimentel, 1976). In cases where insect population increases occur on phenoxy-herbicide treated plants, it involves insects whose feeding strategies enable them to exploit the chemical changes induced by the herbicides. In the examples given in the literature, the sap-feeding insects tapped into the nutrient-rich phloem and boring insects fed on plant tissues that responded in an auxin-like manner to the herbicides (Campbell, 1988).

Plant Growth Regulators

Plant growth regulators have been used to control insects by physically altering the host plant and through influencing the chemical basis of insect-plant interactions. An extensive list of the effects of PGRs on various insect species on different plant species is given in Campbell (1988). Defoliants are used to remove food sources of insects, such as cotton bolls, to reduce the overwintering of the pink bollworm (*Pectinophora gossypiella* Saunders) (Adkisson, 1962). The strategy is to starve the larvae before they enter diapause. Pear trees were treated with daminozide to control the pear psylla, *Psylla pyricola* (Foerster). By retarding shoot growth of pears, psylla populations were reduced 35% and fruit damage 57%, and yields increased (Westigard *et al.*, 1980).

Attempts to control insects by changing host plant chemistry with PGRs are limited. Chlormequat chloride (CCC) has received extensive interest for its effect on reducing aphid infestations on cereals. CCC is commonly used in Europe as an antilodging agent for wheat and barley. In most cases where CCC is used, there is a reduction in the herbivorous insects. Van Emden (1964) reported that CCC reduced aphid populations on brussel sprouts. The reduction was reported to be due to decreased levels of free amino acids in CCC-treated plants (van Emden & Wearing, 1965). Later studies indicated that the effect of CCC on aphid-plant interactions may be due to changes induced by CCC on plant intercellular pectin (Dreyer & Campbell, 1984). Ingestion of phloem sap by aphids on sorghum was associated with the rate that the aphids could break down host plant pectin. It has also been shown that CCC alters

the pectin chemistry of wheat. Wheat treated with CCC had an 80% increase in pectin (Blaim & Przeszlakowska, 1967) and altered the chemistry of pectin substances (Blaim *et al.*, 1970). Structural changes in pectin also affect feeding behavior. Breakdown products from the action of aphid polysaccharases on cell wall polysaccharides act as probing cues for host plant recognition. Thus, PGR-induced changes in the structure of these polysaccharides will influence the gustatory responses of aphids (Campbell, 1988).

Campbell (1988) has summarized the potential of using PGRs in IPM programs. The use of PGRs to alter plant chemistry has significant applied potential in the control of insect pests. Such a strategy would be a means of controlling insects without the adverse side effects against non-target insects such as predators and parasites. In addition, PGRs could be used to induce resistance in agronomically suitable but insect susceptible cultivars without having to rely on long-term breeding programs or develop insect resistant cultivars. The PGRs can be used to improve fruit set, flowering, taste, and harvesting, and simultaneously make crops resistant to insect attack or change the life cycle of the pest to increase its exposure to adverse climates and biotic agents.

Air Pollution

Air contaminants are classified as primary pollutants which are emitted from combustion and industrial processes, or secondary pollutants that are products of chemical reactions in the atmosphere between primary pollutants and hydrocarbons in the presence of sunlight. Primary pollutants most often affect vegetation in localized areas because they are produced by point sources and their concentration away from the source is reduced by dilution and dispersion. Secondary pollutants are more important locally because they are produced throughout the air mass. The book by Treshow and Anderson (1989) covers the effect of the various pollutants on plants. Hughes (1988) described in detail the various air pollutants and their effects on plant-insect interactions.

Table 2 lists the most important naturally occurring and anthropogenic air pollutants. SO₂ is the world's most important air pollutant being produced in large quantities by coal and oil combustion and by industrial processes. Fluorides, emitted by volcanoes and produced from coal combustion and industrial processes, have the important property of accumulating in plants. Secondary pollutants, also called

photochemical oxidants, include oxides of nitrogen, ozone, and peroxyacyl nitrates. Oxides of nitrogen are produced both anthropogenically and biologically. O_3 is considered to cause more plant damage in the U.S.A. than any other pollutant. Acidic precipitation has become an increasingly important air pollutant in recent years. Acidic precipitation results mostly from oxides of sulfur (primarily from the burning of coal and petroleum products) and oxides of nitrogen (primarily from transportation vehicles).

Hughes (1988) has listed the sensitivity of various plant species to pollutants. Barley is sensitive to SO_2 , NO_2 , and O_3 and has an intermediate sensitivity to PAN. The level of sensitivity of a plant species to a particular pollutant is important in that it determines whether plant exposure to the pollutant is likely to alter plant metabolism sufficiently to affect insect-plant relations. The sensitivity of a plant to pollutants depends on the particular pollutant, plant species, plant stage, environmental conditions, and the other pollutants to which it is exposed. The major mechanisms by which pollutants alter plants as hosts for insects are described as follows.

Host Plant Vulnerability to Discovery

Pollutants cause color changes in plants that affect the orientation of insects (Malhotra & Blauel, 1980). SO_2 -induced increases in terpene in balsam fir trees affects host location by insects (Wood, 1982). Plant apparency and availability are altered by pollutant-induced changes in plant species diversity or by changes in availability of a particular plant structure on which a particular insect species depends.

Nutritional Quality of Host Plants

Pollutants cause changes in plant nutritional quality in several ways. Acidic deposition lowers soil pH affecting microbial activity involved in nutrient cycling (Klein & Alexander, 1986); microbes involved in biological nitrogen fixation are sensitive to pollutants; and some metals serve as needed nutrients for plants (Nyborg, 1978). Nutritional quality of plants is also altered by pollutant-induced changes in levels of primary and secondary metabolites. Free amino acids and organic acids generally increase in plants exposed to moderate concentrations of pollutants, while sucrose and foliar lipids tend to decrease (Hughes, 1988).

Secondary plant metabolites affecting the acceptability or quality of plants as hosts for insects are affected by air pollutants. Flavonoids which inhibit

insect growth increase in alfalfa foliage exposed to O_3 (Jones & Pell, 1981), and allelochemicals that alter insect behavior, such as phenolics, increase in trees exposed to SO_2 (Grill *et al.*, 1975). Pollutants can alter the nutritional value of plants in additional ways, as described by Hughes (1988).

Host Defenses

Pollutants affect plant defenses against herbivorous insects by affecting plant surface morphology, leaf toughness, and secondary metabolites that serve as defenses against insects. Pollutants affect the production of phytoalexins that deter herbivory.

Although numerous studies have shown that pollutant-induced changes in host plants affect insect populations, little is known about the specific mechanisms involved. Generally, sucking insects (especially aphids) and secondary pests (those for which a plant is a marginal host) are the most commonly affected (Hughes, 1988).

Mechanical Damage

Mechanical stresses on plants involve natural environmental factors (climatic extremes), such as wind, dust, lightning, hail, sleet, and snow, and those stresses caused by man and animals (including herbivorous insects). Mechanical stresses caused by man and animals result from wounding of plant parts and mechanical perturbations, such as shaking, rubbing, and bending (Heinrichs, 1988). Thigmomorphogenesis is a plant growth and developmental response resulting from mechanical perturbations, such as wind stress and rubbing (Jaffee & Biro, 1979).

Plant Wounding

Reviews by Rhoades (1979) and Edwards and Wratten (1983) note that wound-induced responses in plants resulting from mechanical damage are part of a general defensive reaction, as wound-evolved phytochemicals are similar to those developed during pathogen infection. Edwards and Wratten (1983) classified responses of plant tissues to wounding as: (1) chemical changes of cells, (2) changes in cells adjacent to the damaged tissue, and (3) generalized changes in a plant part or the entire plant.

Plant wounding in this discussion will refer to plant tissue abrasion, cutting, or tearing as the result of mechanical damage or from insect feeding that causes similar injury symptoms. Wounding causes rapid changes in protein, lipid, and phenol metabolism and production of a wound hormone, "traumatic

acid" (Smith, 1988). Phytochemicals produced act as defensive compounds against insect attack or may induce herbivory, depending on various interacting factors. A plant may become more susceptible or more resistant as the result of wounding.

Host selection by the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), is associated with the level of phenols in wheat (Leszczynski *et al.*, 1985). Aphid feeding affects the phenol content of wheat cultivars. Mechanical damage also stimulates enzymatic reactions that release phytochemicals detrimental to insects. Cyanide released as hydrogen cyanide in damaged tissues of sorghum and cassava causes resistance to grasshoppers (Bernays *et al.*, 1977). There are several examples of tree species that have increased resistance to insects after being exposed to insect feeding damage (Smith, 1988). Many appear to be related to increased phenol levels as a result of feeding damage.

Mechanical damage to plant tissue increases plant susceptibility to some insects. Grasshoppers were observed to prefer damaged leaves or inflorescences of the wild sunflower (Lewis, 1984). Defoliation of grand fir, *Abies grandis* Douglas (Lindley), decreases monoterpene content which predisposes trees to attack by the fir engraver beetle, *Scolytus ventralis* (Wright *et al.*, 1979). Root pruning of loblolly pine during timber harvest, or root damage by wild pigs, increased the susceptibility to the southern pine beetle (Hetrick, 1949). Root wounding reduces the total resin flow in pine trees, making them less able to impede beetle attack.

Thigmomorphogenesis

Thigmomorphogenesis (rubbing or bending of plant parts) is similar to wound-induced phytochemical production and is translocatable between internodes. Endogenous ethylene is believed to mediate thigmomorphogenesis (Jaffee & Telewski, 1984). Wounding of plants serves a distinct chemical response which influences insect populations. The release of airborne cues by damaged plants has been reported to stimulate biochemical changes in adjacent plants which in turn influence the feeding and growth of phytophagous insects (Baldwin & Schultz, 1983). These have been referred to as the "talking trees." Plants wounded by insect feeding generally have an enhanced level of tolerance to other stresses, including mechanical stress, and to other insects.

Plant Pathogens

There is a great deal of literature concerning the theory and mechanisms of plant-disease and plant-insect interactions. However, little is known about the specific changes occurring in plants under phytopathogenic stress and their subsequent effects on herbivores utilizing the plants as hosts. Diseased plants function in a capacity defined as an altered host, and any influence of the pathogen on an insect herbivore is exerted indirectly through modifications in host plant morphology, physiology, and plant population dynamics (Bridges *et al.*, 1985).

Phytopathogenic diseases can produce a number of symptoms that modify or disrupt plant morphology. The most common symptoms are leaf chlorosis, wilting, reduced vegetative proliferation, defoliation, stunting, gall formation, and necrosis (Dickinson & Lucas, 1982). All of these changes in plant morphology can affect plant-insect interactions.

Plant pathogens alter plant chemistry, resulting in changes in the nutritional value of plants as hosts for insects and in the level of allelochemicals which alter insect behavior (Whitman, 1988). The plant-pathogen-insect interactions involving viruses and fungi are described in Hammond and Hardy (1988).

Viruses

The effects of plant viruses on their respective insect vectors, and on nonvectors, range from beneficial to lethal (Jensen, 1969). Direct effects of the virus on its vector, and indirect effects of the virus through the diseased host plant, are often difficult to separate.

Plant-mediated effects of viral infection on herbivorous insects are listed by Hammond and Hardy (1988). Insect responses include changes in feeding preference, fecundity, survival, alate production, and population growth. Markkula and Laurema (1964) reported a positive correlation between aphid fecundity and higher levels of amino acids on barley yellow dwarf (BYDV) infected plants. Ajayi and Dewar (1982, 1983) reported that digestibility by the aphid *Sitobion avenae* (F.) on BYDV-infected plants differed from that on uninfected plants. They suggested that reduced honeydew excretion by aphids on cereals infected with BYDV implies nutritional superiority of infected plants. Miller and Coon (1974) found increased fecundity and longevity of the aphid *Macrosiphum granarium* (Kirby) on BYDV-infected oat plants, while Gildow (1984) reported increased alate production of the aphid *S. avenae* on BYDV-infected

oats. Laurema *et al.* (1966) showed that longevity of aphids on oat plants infected with European wheat striate mosaic virus was significantly reduced and, as a result, fewer progeny were produced (Figure 3).

Fungi

Nearly 8,000 fungal species are known to cause plant disease (Lucas *et al.*, 1985). These include the economically important rusts and smuts, powdery and downy mildews, and blights. Most plants, when infected with a fungus, function in an altered host capacity, becoming more or less favorable to herbivorous insects. There are numerous reports of insect-fungus-plant interactions associated with trees. The southern pine beetle, *Dendroctonus frontalis* (Zimmermann), is associated with the blue-stain fungus, *Ceratocystis minor* (Hedgecock), in pine. Among the phytopathogenic effects of the fungus are xylem disruption and subsequent reduction in tree water content, believed to be essential for beetle brood production (Nelson, 1934). White pine (*Pinus monticola* Douglas) trees weakened by the crown-defoliating blister rust, *Cronartium ribicola* (Fisch.), were susceptible to root pathogen invasion which subsequently incited bark beetle establishment (Kul'havy *et al.*, 1984). Although the relationship between insects and phytopathogenic fungi in arboreal systems has been extensively studied for bark beetle-associated diseases, other associations are poorly understood (Hammond & Hardy, 1988).

Few observations of insect association with plant-fungus complexes in cultivated crops have been documented. European corn borer (*Ostrinia nubilalis* Hübner) larvae had increased growth rates when reared on maize infested with the anthracnose fungus *Colletotrichum graminicola* (CCS). They postulated that fungal activity may catabolize complex carbohydrates to more easily assimilated sugars.

The presence of endophyte infection in grasses has been shown to be detrimental to insect herbivores feeding on these grasses. Endophyte-mediated resistance is well established in perennial ryegrass (*Lolium perenne* L.). Crickets feeding on infected ryegrass suffered 100% mortality in less than four days (Ahmad *et al.*, 1985). Reduced damage of ryegrass cultivars to soil webworm (*Crambus* spp.) and the grass billbug (*Sphenophorus parvulus* Gyllenhal) is due to the presence of endophyte in the plant tissue (Funk *et al.*, 1983; Ahmad & Funk, 1983). Deleterious effects of endophyte infection in the fall armyworm, *Spodoptera frugiperda* (J.E. Smith), are a

decrease in the feeding, survival, and developmental parameters (Clay *et al.*, 1985). Indolic alkaloids have been suggested as compounds having antibiotic effects on insects feeding on endophyte-infested ryegrass (Rowan & Gaynor, 1986).

Numerous other plant-pathogen-insect interactions involving viruses, mycoplasma, bacteria, and fungi have been reported in the literature. The reader is referred to Hammond and Hardy (1988) for an in-depth treatment of this subject.

Conclusion

There is strong evidence of changes in insect responses induced by abiotic and biotic stresses, but the ecological significance of such changes is limited. While most of the studies have looked at the short-term responses of insects, few have considered the long-term effects on population dynamics. Field studies indicate that plant stresses cause outbreaks of secondary pests and a change in the frequency and extent of outbreaks of species with cyclic patterns of eruption. Stresses that have a dual effect of reducing parasitism and predation and increasing the suitability of plants as hosts for insects are extremely important in the population dynamics of herbivorous insects (Riemer & Whittaker, 1989).

With the increases in the human population and the resultant decrease in cropland area, soil deterioration, ground water depletion, air pollution, possible long-term changes in climate, and other plant stress factors will be a continuing and increasingly severe threat to the quality of life in both the developed and developing countries. Because of the limited amount of fertile, uncultivated cropland, gains in production will come from increased yields and utilization of marginal lands. To utilize marginal lands which impose severe stresses on plants, they must be modified to make them suitable for crop production, or the crop plant species must be genetically modified to tolerate stress conditions.

The greatest gains in crop production are expected to come from the modification of the plant genome to allow plants to tolerate stress, rather than through a modification of the plant's environment. These gains will occur through conventional plant breeding techniques and through techniques involving molecular genetics. The modification of genes which alters plants' ability to withstand various abiotic and biotic stresses will often affect their suitability as hosts for insects. In the breeding of stress-resistant crop cultivars, the level of susceptibility to insects must be closely monitored so as to select lines with

equal or preferably higher levels of resistance than currently grown commercial cultivars. Also, the development of insect-resistant crop cultivars should include the evaluation of breeding lines for tolerance to other stresses. The failure to do so could result in the release of cultivars that are highly susceptible to insect pests and other stresses.

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TABLE 1. Plant compounds induced or increased by light.*

Plant compound	Light source	Plant source
Alkaloids	Red and IR	Tobacco
Alkaloids	Visible	Lupines
Alkaloids	UV	Various solanaceae
Anthocyanins	Visible	Many plants
Betacyanins	Red	Centrospermae
Cannabinoids	UV	Marijuana
Carotenoids	Blue	Many plants
Cardenolides	Visible	<i>Digitalis lanata</i>
DIMBOA	Visible	<i>Zea mays</i> L.
Flavonoids	UV	Many plants
Furanocoumarins	UV	Wild parsnip
Isoflavonoids	UV	Soybeans
Tannins	"Sunlight"	Oak
Terpenes	"Sunlight"	<i>Hymenaea courbaril</i> L.

*From Berenbaum (1987).

TABLE 2. Partial list of naturally occurring and anthropogenic air pollutants.*

SULPHUR DIOXIDE	MISC. PHYTOTOXIC POLLUTANTS
FLUORIDES <ul style="list-style-type: none"> Hydrogen fluoride Silicon tetrafluoride Calcium fluoride Cryolite 	<ul style="list-style-type: none"> Unsaturated hydrocarbons Agricultural chemicals Hydrogen chloride Ammonia Hydrogen sulfide
PHOTOCHEMICAL OXIDANTS <ul style="list-style-type: none"> Ozone Oxides of nitrogen Peroxyacetyl nitrate (PAN) Ambient oxidant complex 	PARTICULATES <ul style="list-style-type: none"> Heavy metals Dust Volcanic ash Acidic precipitation

*From Hughes (1988).

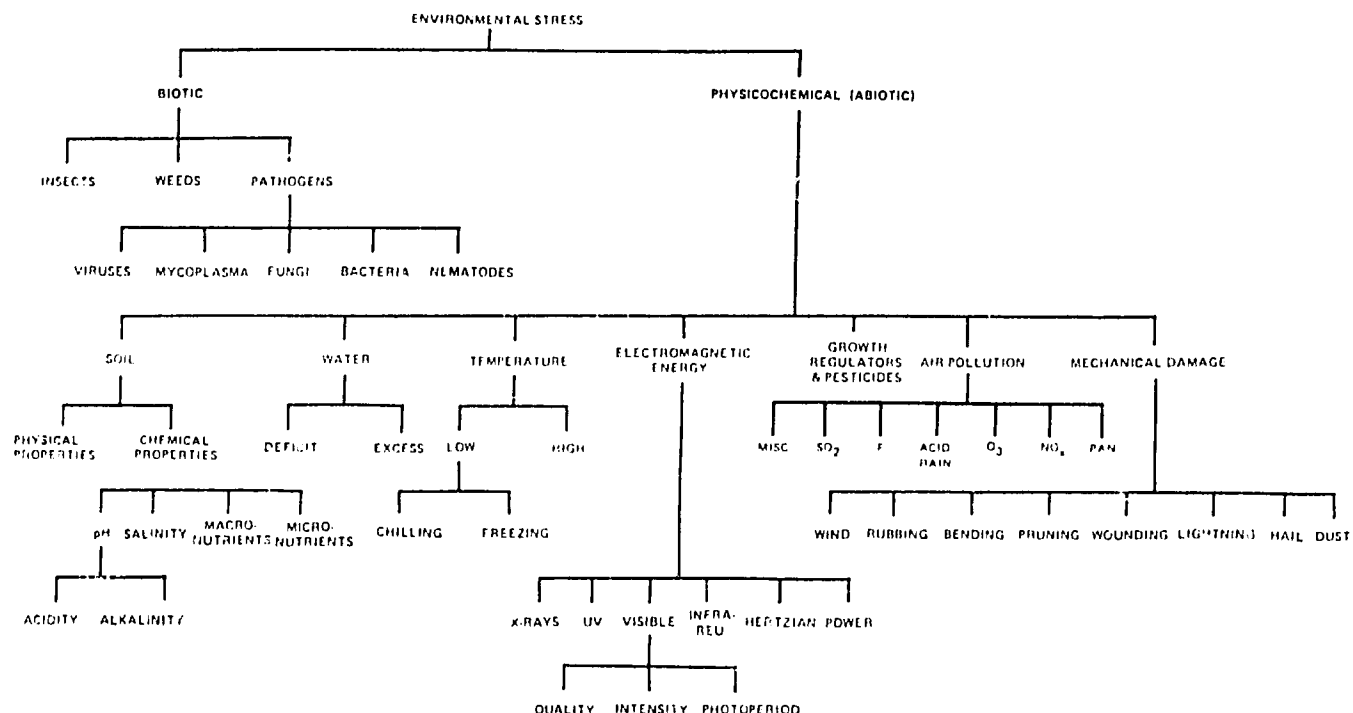
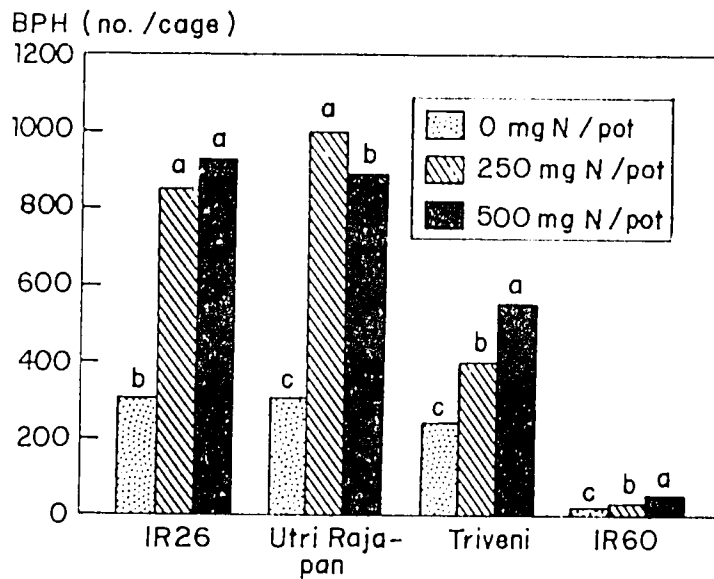
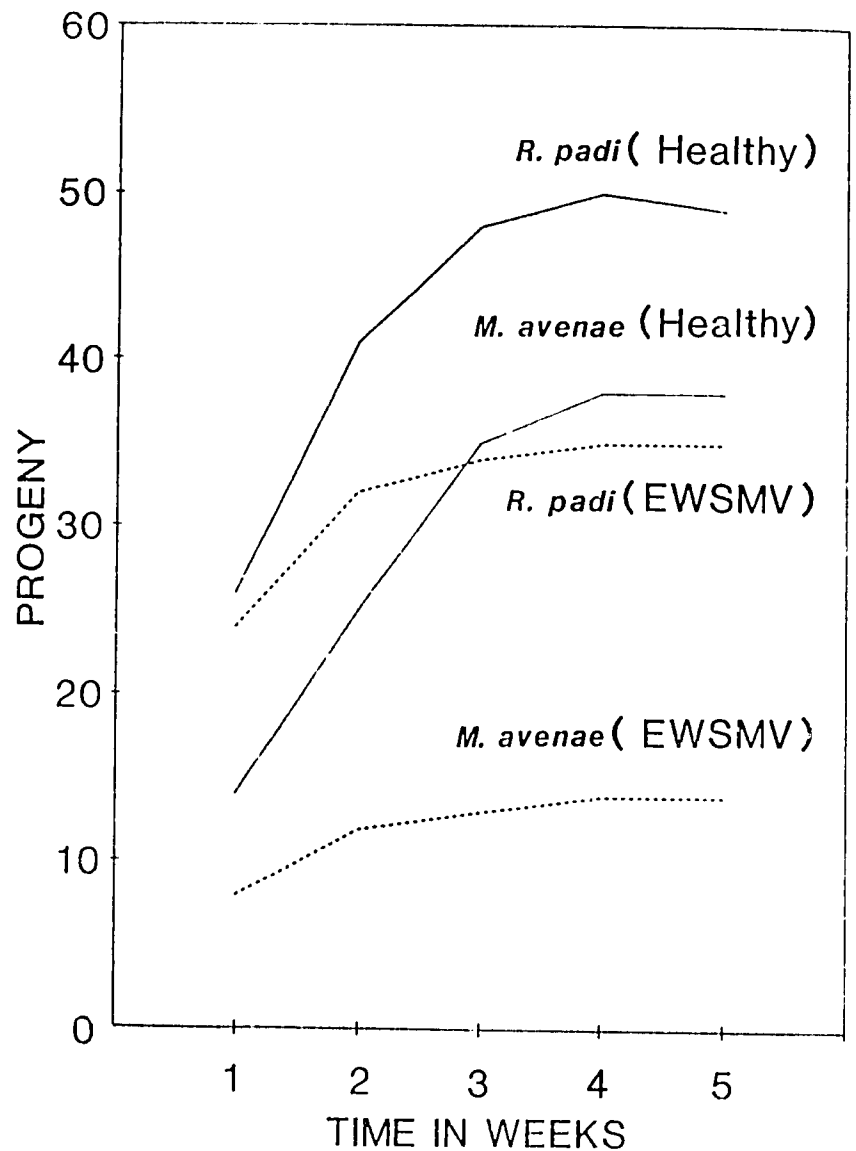


FIGURE 1. Types of environmental stresses to which a plant may be subjected. (Heinrichs, 1988, modified after Levitt, 1972)

**FIGURE 2.**

Brown planthopper (BPH) *N. lugens* biotype 2 population growth on selected rice varieties grown under N fertilizer $[(\text{NH}_4)_2\text{SO}_4]$ rates. IR26 susceptible to *N. lugens*, Utri Rajapan has tolerance but no antibiosis, Triveni has moderate levels of tolerance and antibiosis, and IR60 has high levels of antibiosis. Bars within a variety with the same letter are not significantly different at the 5% level by Duncan's multiple range test. (From Heinrichs & Medrano, 1985)

**FIGURE 3.**

Progeny production of healthy and European wheat stripe mosaic virus infested oats by the aphids *Rhopalosiphum padi* L. and *Macrosiphum avenae* (F.). (Modified after Laurema et al., 1966, by Hammond & Hardy, 1988)

Influences of Biotic Stress on Barley Production: Interactions Between Diseases and Drought

P. G. Ayres*

Interactions between drought and disease have rarely been studied in the field, so the extent to which their effects are additive is uncertain. Fungal structures are often poorly adapted to growth in arid environments. Even for the best adapted pathogens, growth is depressed under dry conditions, probably because the fungus must divert more resources to osmoregulation in order to maintain a water potential lower than that of its host. Foliar pathogens affect transpiration per unit of shoot area, some causing an increase, others a decrease. Their main effects are reductions in shoot area and root mass, the former leading to reduced water consumption per plant and often being sufficient to maintain shoot water potentials close to those of healthy controls under experimental conditions. Water-use efficiency is reduced by foliar infection. Effects on root growth are probably most serious when plants grow in mixture with healthy plants of the same or other species, e.g., weeds, and may result in lowered shoot water and turgor potentials. As with disease caused by rhizopathic fungi, about which even less is known, the effects of foliar pathogens may depend on the pattern of soil drying in relation to the distribution of the remaining root system.

Introduction

The interactions among drought, plants, and pathogens can be conveniently represented by a form of the well-known "disease triangle" (Figure 1). While drought and pathogens each tend to reduce plant growth, it is possible that together their effects may be synergistic, additive, or even counteractive. Indications come occasionally from farming practices, but in the notable absence of field experiments specifically to test these alternatives, evidence as to which is correct comes mainly from glasshouse and laboratory experiments designed to explore particular aspects of the triangle. The latter are the source of evidence discussed here.

The diseases focused on are powdery mildew (*Erysiphe graminis* f.sp. *hordei*), rusts (mainly

Puccinia hordei), and take-all (*Gaeumannomyces graminis*). The first two are ubiquitous foliar pathogens and probably the most economically important diseases of barley. Take-all is included, in spite of its occurrence in wetter rather than drier soils, because it is the only root disease of cereals upon which a significant amount of research has been done and it is used to illustrate some general principles. The limited literature means that information is often derived from studies of wheat and other cereals, rather than barley (particularly in the discussion of take-all), and occasionally of dicotyledonous hosts.

Two aspects of the triangle are selected for special consideration. First is the effect that drought may have on the growth of the fungus once it has established a compatible relationship with the host. It should be remembered that the effects of drought on the development of the plant may also affect its susceptibility to infection, i.e., predisposition (e.g., Ayres & Woolacott, 1980), but space does not permit exploration of this extensive subject. Second, the effects that disease may have on water consumption by the plant, i.e., on the environmental resource, soil water, is considered. The pathogen may also affect water in the atmospheric environment by, for example, reducing leaf growth and promoting the movement of dry air through the crop, but evidence is lacking here.

Water Relations of Fungi

There is much similarity between the water relations of plant cells and fungal hyphae. Water is needed in both for expansion, which occurs when the turgor pressure potential exceeds the yield turgor of the wall, particularly in fungi, the wall at the hyphal apex. To maintain water uptake, a fungus must have a water potential lower than that of its environment, whether that is the soil or living host tissue. This requires that the fungus be able to accumulate

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osmotically active solutes. However, although it is clear that solute regulation in response to environmental water stress can occur through the increased accumulation of solutes such as glycerol and mannitol, little is known of the mechanisms by which the growth of pathogenic fungi responds to drying environments or the effects that any responses may have on their pathogenicity. While the effects of environmental water, both free and in the atmosphere, on the sporulation of foliar pathogens and storage fungi are relatively well documented, other areas of pathogen water relations are poorly researched. For example, there is a surprising lack of information on both the water relations of sclerotium formation by soil inhabiting fungi, and the survival of sclerotia and spores.

Pathogens That Can Be Cultured *In Vitro*

By regulating the osmotic, or sometimes the matric, potential of the medium, researchers have found that growth of the many pathogens that can be cultured *in vitro* typically decreases with decreasing osmotic potential, although there are differences between species and between isolates of the same species. Root infecting fungi generally fall into a group of medium sensitivity the members of which are able to maintain growth at water potentials down to approximately -4.5 to -7.5 MPa. Growth *in vitro* of isolates of *Gaeumannomyces graminis* var. *tritici* (take-all) was reduced by 50% at -2.0 MPa and ceased below -6.0 MPa (Table 1); that of *Fusarium graminearum* ceased only at -7.7 MPa (Wearing & Burgess, 1979). Ability to grow at low water potential is often correlated with the geographic distribution of a pathogen. Thus, take-all is not serious in wheat under dryland conditions where water potentials are commonly at -2.5 to -3.5 MPa, and occasionally reach -5.0 MPa (Cook, 1981). Where lack of correlation arises, it is because other factors, such as inoculum survival between host growing periods and host resistance, are differentially affected by drought, or the growth of antagonistic or competitive microorganisms may be less sensitive than that of the pathogenic species to drought.

Pathogens That Cannot Be Cultured *In Vitro*

Field observations show that powdery mildews are remarkably tolerant of, if not favoured by, dry conditions (Yarwood, 1978). Powdery mildew like rusts cannot be grown away from host tissue, which places severe limitations on our ability to investigate their water relations. Nevertheless, by stressing host

plants, we can show that even for such a comparatively well adapted fungus, a reduction in environmental (plant) water potential inhibits mycelial growth (Ayres, 1977), increases the latent period, and reduces numbers of conidia produced per day (Figure 2).

It is becoming apparent that mildews have a number of unusual stratagems that contribute to their exceptional drought tolerance. For example, under humid conditions each conidium of barley mildew germinates by first producing a very short primary germ tube (PGT), followed somewhat later by a larger germ tube that gives rise to a voluminous appressorium from which an haustorium may be established in the underlying epidermal cell. Carver and Bushnell (1983) have shown that the PGT may be essential in arid environments as a channel for water uptake (Figures 3a,b). Conidia that either failed to attach naturally, or whose PGTs were detached early by micro-manipulation, failed to develop further in an arid environment but often gave rise to normal infections in a humid environment. Aridity also increased the number of PGTs naturally attached to the leaf surface.

Spores are most prone to desiccation when they have no direct connection with parent mycelium or host tissues. The conidia of powdery mildews appear unusually well equipped to cope with this stress. Those of pea mildew (*Erysiphe pisi*) have a waxy surface, reminiscent of the cuticle of leaves, and like those of barley mildew are remarkably impermeable (Gay *et al.*, 1985). Conidia of barley mildew produced in a dry environment (32% r.h., 20°C) were able to retain visibility for relatively long periods, e.g., 6 h at 50% r.h. (Ward & Manners, 1974). Caesar and Clerk (1985) reported that 5% of conidia of *Leveillula taurica* produced from leaves of pepper plants with a relative water content of 48.8% were able to germinate in an atmosphere of 5% r.h. at 26°C. Conidia store water, up to 75% of fresh weight in some mildew species, but they are also rich in lipid reserves; it has been proposed that these are metabolized, producing water, prior to invasion of the host (Yarwood, 1978).

The initial extent of such reserves can be affected by the environment in which spores are produced. We have found that the solute potential of conidia from barley grown under dry conditions was lower (-4.6 ± 0.3 MPa) than that (-3.1 ± 0.1 MPa) of conidia from barley grown under wet conditions (both potentials were lower than those of respective hosts). Conidia taken from dry plants had a greater ability to infect other plants grown in dry soil than conidia taken from plants grown in wet soil (Table 2). This

and the effects of lowered host water potential on spore production and latent period clearly have important epidemiological consequences that have not yet been assessed in the field.

We examined responses to drought further by studying the uptake of ^{14}C sucrose by mycelium of pea mildew on leaf slices. (Pea mildew is easier to study than barley mildew since it may be peeled away from the leaf as a continuous mat.) Although air movement over the leaf promoted carbon transport into the fungus, probably because it promoted turgor pressure gradients, and thus mass flow from intra-cellular haustoria to superficial mycelium, stress during incubation inhibited transport, probably because it depressed those gradients. The main effects were seen if plants were drought-stressed before the experiment, and particularly if that stress was continued during the experiment. Increased carbon was taken up by the leaf, but there was a decrease in the percentage of total ^{14}C taken up that was transferred to the mycelium (Table 3). Since osmoregulation competes with growth for raw materials, it is suggested that this competition contributes to the reduced carbon transport to the fungus, and, ultimately, the reduction in mycelial growth and sporulation seen in stressed mildewed plants. It may be relevant that mildew infection stimulated the normal accumulation of proline in drought-stressed barley (Bielka & Bielka, 1988), and of proline and glycine-betaine in salt-stressed barley (Murray & Ayres, 1986). Such changes would tend to deprive the fungus of carbon and nitrogen, particularly if, as Murray and Ayres (1986) suggested, these solutes cannot be metabolized by the fungus.

The Water Relations of Infected Plants

Root-Infecting Pathogens

There is very little information on the effects of root-infecting fungi on plant water relations. Martin, Mathre, and Johnston (1986) found that Water Transpired and Water-Use Efficiency in winter wheat were both reduced by infection with *Cephalosporium graminearum*, with water extraction being reduced throughout the soil profile because of either reduced root density or reduced demand for water. Fitt and Hornby (1978) compared the effects of seven fungi on water and solute transport in wheat. *Aureobasidium bolleyi* and *G.g.t.* damaged the phloem and reduced water content, while *Phialophora radicola*, *Wojnowicia graminis*, and *Pythium scleroteichum* did not penetrate steles and did not affect the shoot.

Asher (1972) noted that leaves of wheat infected by take-all had a lower percentage water content than controls. Kararah (1976) found that 10 days after inoculation, isolated seminal roots took up 2% of the water taken up by control roots. The xylem had been invaded by the fungus at this stage, but it was not clear whether radial or axial transport of water was interfered with. A critical event in the development of take-all is invasion of the phloem since this is followed within two to three days by cessation of the upward transport of xylem-mobile ions, and presumably of water, and the failure of root elongation (Clarkson *et al.*, 1975).

The immediate effects of rhizopathogens depend on the position of their infection site(s), whether near the root tip or base, for within the plant there is scope for increased compensatory water uptake in other, healthy roots. In the longer term, impaired root function affects shoot function and the production of new roots. Asher (1972) observed 30% reductions in the dry weight of wheat roots caused by take-all infection, although there was an increase in the root:shoot ratio from 0.45 in healthy to 0.56 in infected plants. Barley has a greater capacity than wheat to replace diseased roots, which may explain reports that its yield is reduced less than that of wheat when the same amount of root shows disease symptoms.

There is only piecemeal information on the effects of rhizopathic fungi on plant water relations. Although growth of the pathogen may be checked in dry environments, it must be inferred that the damaging effects will be exacerbated. As discussed below for foliar pathogens, the effects of rhizopathogens on root growth and function may put diseased plants at the most serious disadvantage where they compete for a limited soil water supply.

Foliar Pathogens

A pathogen that alters stomatal and/or cuticular resistances to water vapour diffusion away from the leaf has the potential to alter the transpirational flux of water through the plant. In addition, flux may be affected because the dry mass of the root system is reduced. The latter occurs because of changes in carbohydrate partitioning, arising *inter alia* from inhibition of net photosynthesis at the infection site as the result of increased stomatal and/or mesophyll resistance to CO_2 , and because of the nutritional demand of the pathogen. Although there may be a proportional decrease in leaf area, the reduction in the absolute size of the root system will have an adverse effect on plant water relations; it will tend to

increase the perirhizal resistance to water flow across the root surface where the small root system is confined to upper regions of a downward-drying soil profile and/or where infected plants are mixed with healthy plants of the same (crop) species or with weeds.

Rust fungi grow within the leaf, but at sporulation they erupt through the cuticle. Not surprisingly, Ower, Farrar, and Whitbread (1981) reported that in barley infected by *Puccinia hordei*, between the day before sporulation (7 days after inoculation) and the day after sporulation commenced (8 days), the diffusion resistance of leaves fell from 962 to 470 s m⁻¹, while that of controls was relatively constant (763 and 694 s m⁻¹ on 7 and 8 days, respectively). The conclusion that rust infection of cereals causes increased transpiration per unit area of leaf, if water is non-limiting, is abundantly supported in the older literature (see Ayres, 1978); however, it should be noted that those data were derived by indirect, relatively crude measurements of water consumption together with changes in plant dry weight or leaf area, made over long periods on plants grown under greenhouse (Figure 4) or controlled environment conditions. The results could not be consistently corroborated by direct measurements of transpiration for brown rust infected barley (I. Ahmed, pers. communic.). Recent studies of wheat infected by *Puccinia recondita* in our laboratory (S.G. Humphreys, unpublished) show that, at least in newly erupted pustules, the spore mass may effectively block the lesion in the cuticle, thereby increasing the diffusion resistance of the leaf. Rust-induced increases in transpiration have been directly demonstrated, however, for a number of dicotyledonous hosts.

Powdery mildew infection contrasts with rust infection in that the fungus does not tear open the epidermis (its infection structures are tightly sealed to the penetrated epidermal wall). It does, however, inhibit stomatal opening (Figure 5). In seedlings grown in small containers, where difference in the volume of soil exploited by root systems would be unimportant, this inhibition of stomatal opening conserved water to such an extent that in water stressed plants, net photosynthesis and leaf conductance in uppermost uninfected leaves on infected plants were greater than in controls (Figures 6 & 7).

Rusts and powdery mildews have in common their reduction of the transpiring leaf area of the plant. This overrides any effect of leaf diffusion resistance so that when freely watered plants are grown, often to maturity in large containers, rusts (Ayres,

1978), like mildew (Ayres & Zadoks, 1979; Rabbinge *et al.*, 1985), cause a reduction in water consumed per plant (Tables 4 and 5). Second, the different pathogens reduce the ratio between dry matter assimilated and water consumed (Tables 4 and 5). Although Rabbinge *et al.* reported that mildew of wheat did not affect this ratio, their data included a trend for the ratio to decrease as the percentage of the leaf area mildewed increased. Thus, the assimilation:transpiration ratio fell from 10.0 ± 1.0 in controls to 8.9 ± 0.5 in plants with >10% of leaf area mildewed. In the work of Ayres and Zadoks (1979), infection levels reached 75% and the transpiration:assimilation ratio was reduced whether plants were grown in wet soil (highest ratios), medium, or dry soil (lowest ratios) (Table 5). It is suggested that, certainly at high epidemic levels of infection, the effects of mildew and rusts on carboxylation efficiency are more important than any effects on the diffusion properties of the leaf. [In the only comparable study on a foliar pathogen of a grass, Nus and Hodges (1986) report that stripe smut (*Ustilago striiformis*) increased the transpiration:assimilation ratio of leaves of Kentucky Bluegrass (*Poa pratensis*) from 474 to 722 g H₂O g⁻¹ d.wt.] Interestingly, Water Use Efficiency in healthy plants is not altered by stomatal closure in healthy plants and does not normally vary within species (Ludlow & Muchow, 1990).

Effects of rusts and mildew on root growth and function probably are also similar, although in cereals only responses to mildew infection have been studied in any detail. In barley, mildew reduced root mass, length, and the number of branches per unit length of primary root (Walters & Ayres, 1981). The root:shoot ratio is generally reduced, though rather less under stress than well watered conditions (Figure 8). When barley seedlings grown in 50 cm deep soil columns were fed ¹⁴CO₂ seven days after half had been inoculated with powdery mildew, the increased partitioning of assimilates to roots that was caused by drought was inhibited by infection. While total dry matter of roots in the upper driest quarter of the soil profile was more seriously affected by mildew, roots in the middle region of the profile, where most future growth would occur, suffered most in terms of a reduction in supply of newly assimilated carbon. It is noteworthy that parallel studies of root growth in peas infected by powdery mildew (*Erysiphe pisi*) also found that infection reduced root growth in the drier upper regions of the soil profile (Ayres, 1981).

When roots are isolated, as by detopping of the plant, the smaller systems from infected plants may

transport less water than controls [e.g., $6.7 \pm 0.5 \text{ mm}^3 \text{ plant h}^{-1}$ were exuded from detopped barley infected by brown rust (*P. hordei*) compared with $11.5 \pm 3.5 \text{ mm}^3 \text{ h}^{-1}$ from controls (Ahmed *et al.*, 1982)], a difference roughly in proportion to differences in the dry weights of the root systems. However, the force driving water flux through the intact plant is critical and this, in turn, is determined by the transpiring shoot area as well as by the water potential gradient at the leaf surface. Thus, in both barley (see legend to Figure 8) and pea (Ayres, 1981) infected by powdery mildew, reduced root growth did not lead to lower leaf water potentials in infected plants since these had smaller shoot areas than healthy plants and the deeper roots could supply all the water needed by the shoots during the experiment. Water transport through barley roots may have been facilitated because, as noted by Walters and Ayres (1982), mildew may increase their hydraulic conductance, i.e., flux at a constant driving force. There is no evidence that foliar infection reduces the functional efficiency of roots.

By contrast with the laboratory situation, in the field the smaller root system of infected plants may put them at a serious disadvantage when they compete with neighbors for limited soil water. Pathogenic infection clearly reduces the competitive ability of host plants. For example, in replacement series experiments involving mixtures of barley and wheat grown in pots in a glasshouse, Burdon and Chilvers (1977) found that barley had the greater competitive ability when healthy but the lesser ability when in the presence of barley powdery mildew (to which wheat is resistant). The mechanisms through which competition acts are probably several in each combination of competitors, but disturbed water relations, induced by infection, may commonly be one of them. In mixtures of a single seed line of healthy and rust (*Puccinia lagenophorae*)-infected groundsel (*Senecio vulgaris*) grown in the field, the competitive disadvantage of rusted plants was greatly exacerbated when plants were subjected to drought (Figures 1 & 4). Water potentials were lowered by rust infection, particularly in plants grown in dry soil.

Grain yields of crops in water-limited environments can be analyzed in terms of three largely independent identities (Ludlow & Muchow, 1990): Grain Yield = Water Transpired x Water Use Efficiency x Harvest Index.

Evidence has been presented that mildews and rusts reduce Water Transpired and decrease Water-Use Efficiency. These effects alone may be sufficient

to explain the yield losses caused by these pathogens but, in addition, Harvest Index may be adversely affected. This could occur because of the pathogens' capacity to act as a sink for soluble nutrients and because of their depressing effects on root growth and function which may lower host water potentials. These last possibilities remain to be explored.

Conclusion

Both plant and fungal development are inhibited by drought. Laboratory experiments have revealed drought may affect isolated aspects of host or pathogen development, but there is a dearth of evidence from the field where host-pathogen interactions occur. Available evidence suggests that where disease occurs in dry environments, its most important effect may be the restriction of root growth and, in the case of rhizopathogens, of function. Since absorption by roots is a major factor causing soil drying, it may be anticipated that diseased plants will be at greatest disadvantage, i.e., drought and disease will have the most strongly additive effects, where they grow in mixture with healthy plants of the crop or with weeds.

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TABLE 3. Effect of water stress on net uptake of [¹⁴C] sucrose by pea leaf and *Erysiphe pisi* mycelium.*

Pre-incubation stress ^a	Stress during incubation ^b	Net C uptake (ug sucrose mg ⁻¹ d.wt.)		% of total activity in mycelium (Arcsine)
		Leaf ^c	Mycelium ^d	
-	-	0.36	1.35	22.8
+	-	0.60	1.15	12.3
-	+	0.50	1.40	21.2
+	+	0.80	0.59	10.5
L.S.D. (P=0.05)		0.10	0.40	7.2

*From Wyness and Ayres (1987).

^aSoil water potential 0.0 or -0.8 MPa.

^bWater potential of medium 0.0 or -0.7 MPa.

^cDry weight 2.3 (control) or 2.4 mg cm⁻² (stressed).

^dDry weight 0.11 (control) or 0.10 mg cm⁻² (stressed).

TABLE 1. Growth of fungi at various osmotic potentials at 20°C.*

Fungus	Total no. of isolates	No. of isolates capable of growth at osmotic potentials (MPa)				
		-5	-6	-7	-8	-9
<i>Gaeumannomyces graminis</i> var. <i>graminis</i>	10	10	10	9	3	0
<i>G. graminis</i> var. <i>tritici</i>	10	10	6	0	0	0
<i>G. graminis</i> var. <i>avenae</i>	5	4	1	0	0	0
<i>Phialophora graminicola</i>	10	10	10	4	0	0
<i>Phialophora</i> sp.	5	5	4	4	1	0

*From Wong (1983).

TABLE 4. Water used transpiration and assimilation ratios in rust infected cereals.*

		Water used (l)	Transp/Assim (g/g)
Wheat (Weirs, 1924)	Control	6.7	279
	<i>Puccinia graminis tritici</i>	6.4	304
	<i>P. recondita</i>	6.2	277
Wheat (Johnson & Miller, 1934)	Control	104.3	457
	<i>P. recondita</i>	82.2	905
Oats (Murphy, 1935)	Control (85% moisture)	28.6	269
	<i>P. coronata avenae</i>	18.1	527
	Control (50% moisture)	13.5	166
	<i>P. coronata avenae</i>	10.6	344
Wheat	Control	205.0	458
	<i>P. striiformis</i>	191.0	962
Barley (Bever, 1937)	Control	199.0	543
	<i>P. striiformis</i>	193.0	1026
Oats (Amatya & Jones, 1966)	Control	0.1	324
	<i>P. coronata avenae</i>	0.1	444

*All hosts were susceptible and, except for the final entry, were grown in maturity.

TABLE 2. Infectivity of barley mildew conidia from well watered (wet) or droughted (dry: bulk soil water potential, -1.5 MPa) donor plants on watered or droughted recipients.

	Wet recipients (-0.55 MPa)		Dry recipients (-1.70 MPa)		L.S.D. P=0.05
	Wet donors	Dry donors	Wet donors	Dry donors	
Germination (%)*	38.3	36.8	31.8	44.4	4.2
Elongating secondary hyphae (%)*	16.6	15.6	1.3	4.9	3.6
Colony length x breadth (um)	325 x 75	325 x 75	75 x 5	75 x 5	50 x 25

*Angular transformation of percentage from Ayres and Woolacott (1980).

TABLE 5. Water used and transpiration/assimilation ratios in barley^a at three soil water levels and infected by *Erysiphe graminis hordei*.*

	SOIL		
	Wet (0.0 MPa)	Moist (min. 1.5 MPa)	Dry (min. 3.2 MPa)
WATER USED (l):			
Control	4.02	3.12	1.85
Infected at 64d	4.13	3.18	2.09
Infected at 45d	3.67	2.39	1.92
Infected at 26d	2.45	1.76	1.63
TRANSPIRATION/ASSIMILATION (g/g):			
Control	271	262	201
Infected at 64d	292	254	203
Infected at 45d	344	272	236
Infected at 26d	376	297	269

*From Ayres and Zadoks (1979).

^aApprox. growth stage 75, grain filling.

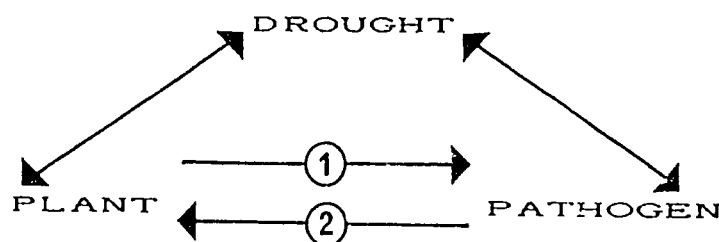


FIGURE 1. Possible interactions between plant, pathogen, and environmental drought. Interactions (1) and (2) are discussed below.

FIGURE 2. Influence of drought stress and plant age on daily spore production by individual colonies of barley powdery mildew. W2 = second leaf of well watered seedling (midday water potential -0.29 ± 0.06 MPa); WA = leaf below flag-leaf on well watered adult plant (-0.71 ± 0.12 MPa); DA = leaf below flag-leaf on stressed adult plant (-0.41 ± 0.06 MPa). (From Woolacott & Ayres, 1984.)

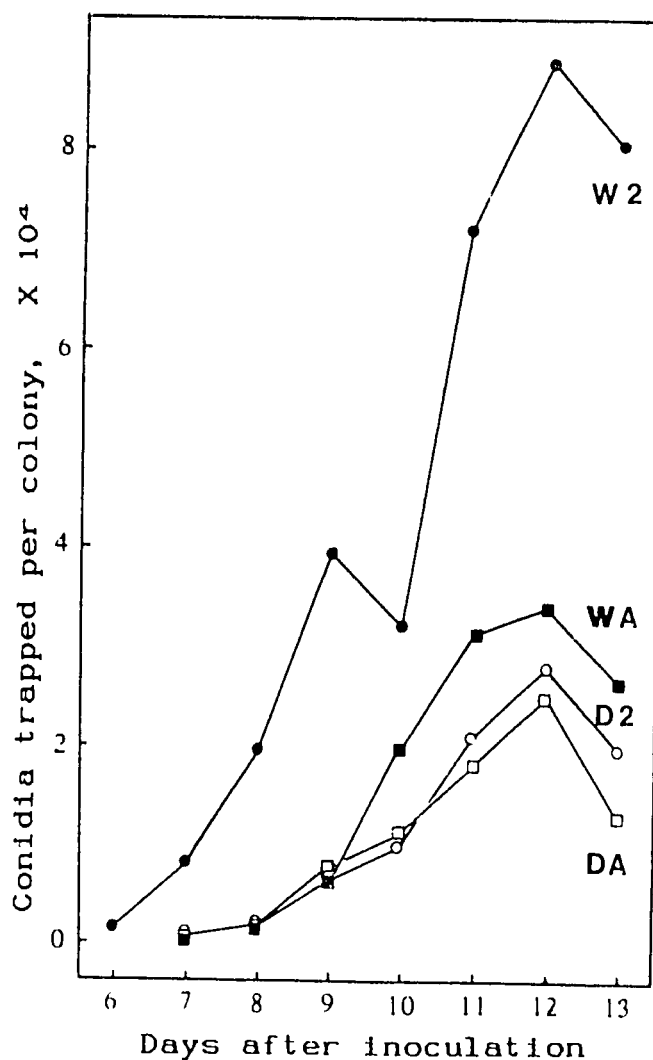


FIGURE 3. Development of barley powdery mildew germlings in (a) humid, (b) dry environment.

○ = attached controls; □ = attached manipulated; ● = unattached controls; ■ = unattached because of manipulation. (i) conidia turgid at manipulation (2-3h); (ii) turgid; (iii) appressorial germ tube formed; (iv) germ tube turgid; (v) appressorium formed; (vi) haustorium formed; n = number of observations. (From Carver & Bushnell, 1983.)

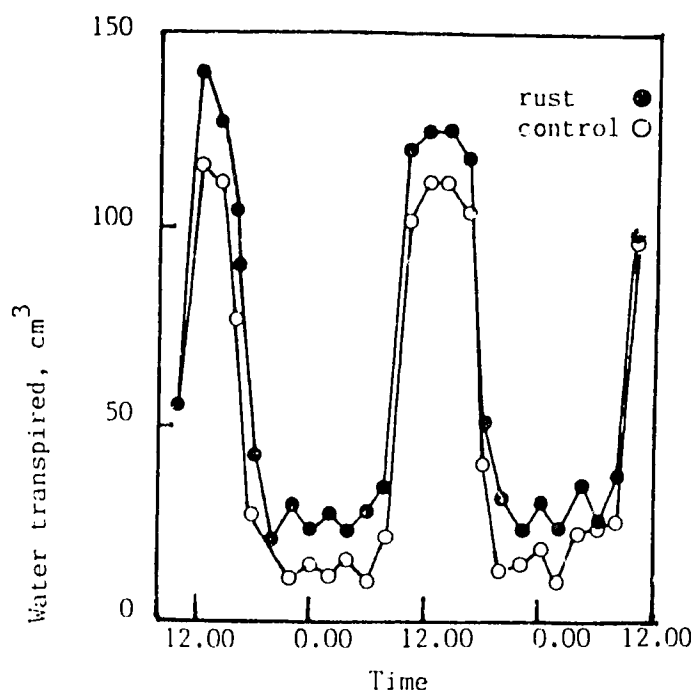
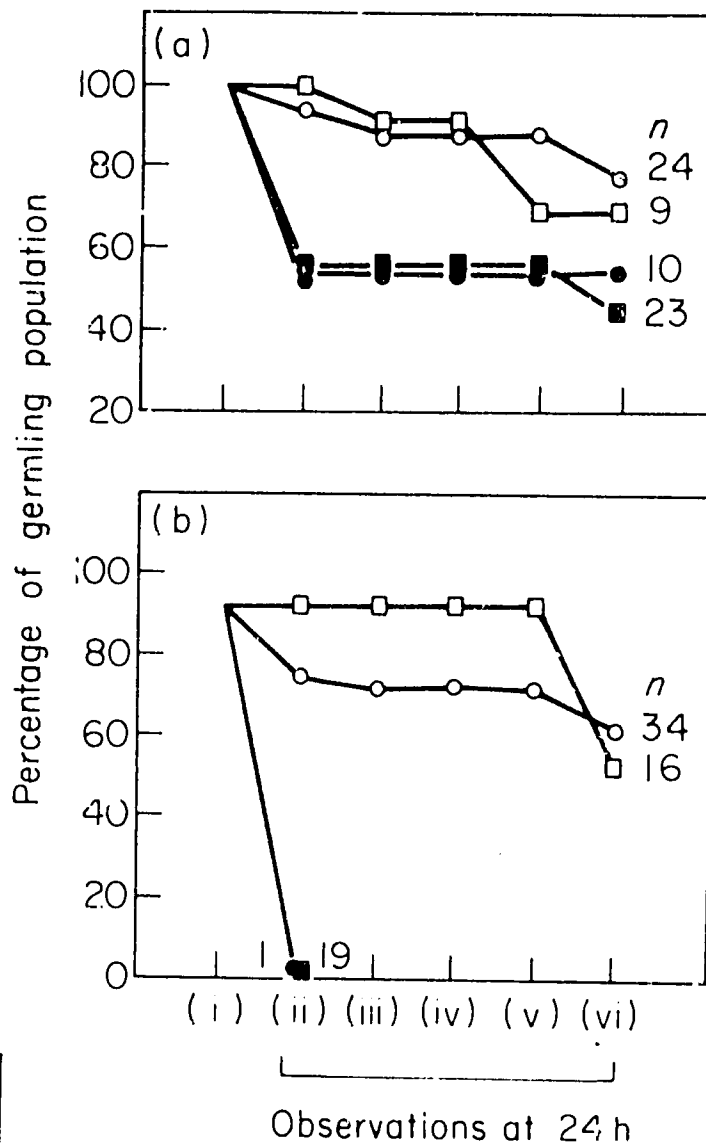


FIGURE 4. Influence of rust (*Puccinia recondita*) on daily patterns of transpiration in wheat. ● = rust-infected; ○ = healthy control. (From Johnston & Miller, 1940.)

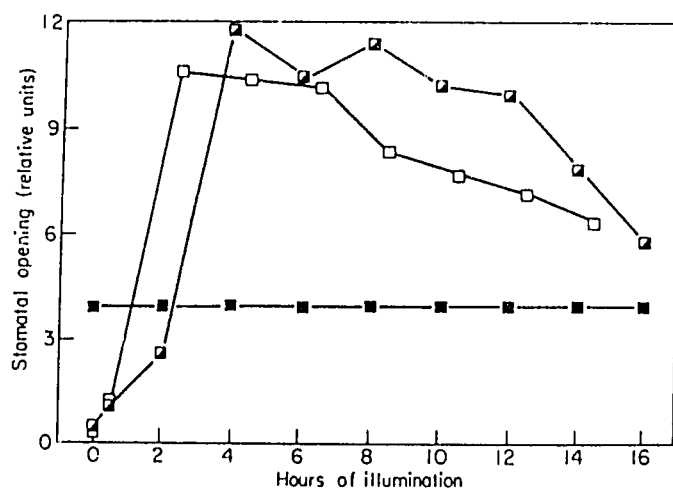


FIGURE 5. Stomatal behaviour in flag-leaves of 55-day-old barley. □ = uninfected; ■ = infected by powdery mildew; ◐ = uninfected region of mildew-infected leaf. (From Ayres & Zadoks, 1979.)

FIGURE 6. Net photosynthesis in healthy third leaves of barley with lower two leaves healthy (○) or infected by powdery mildew (●). Plants well watered (—) or watering stopped on day of inoculation (---). (From Williams & Ayres, 1981.)

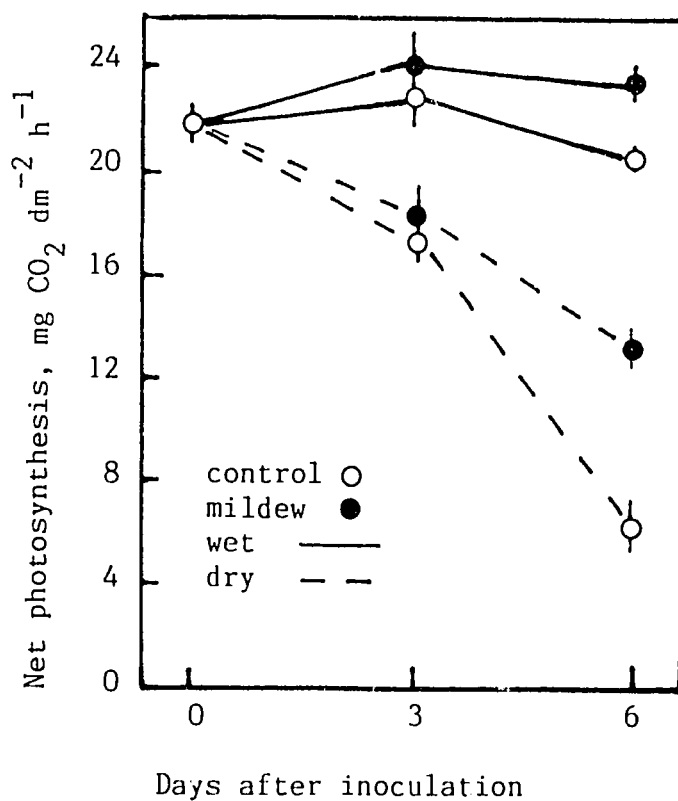
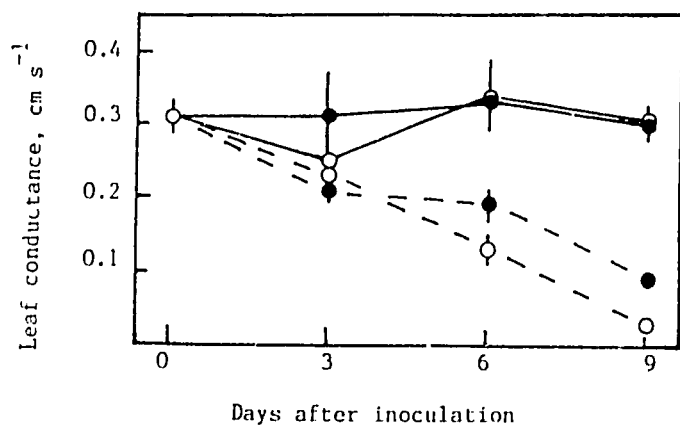


FIGURE 7. Leaf conductance, drought stress, and barley mildew. (See Figure 5 for symbols.)



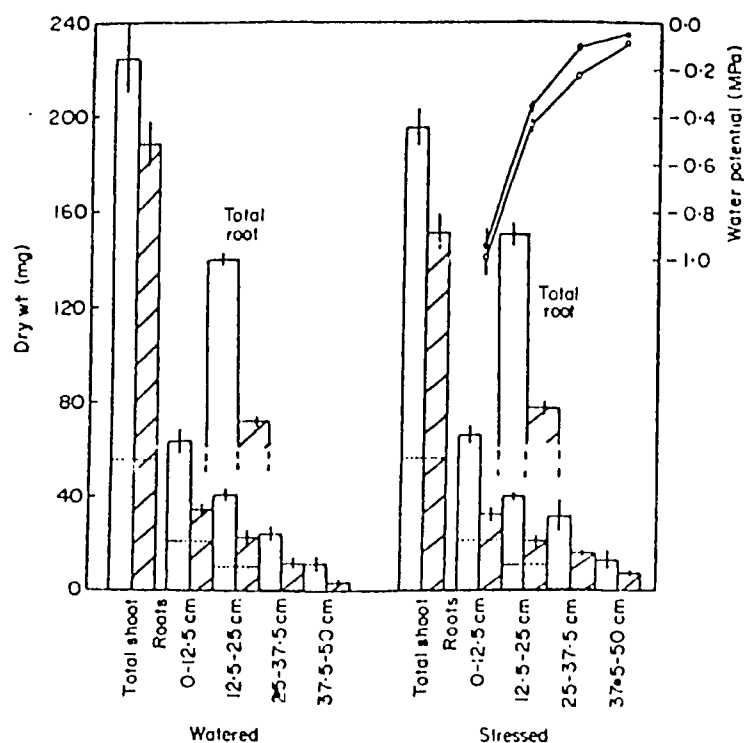
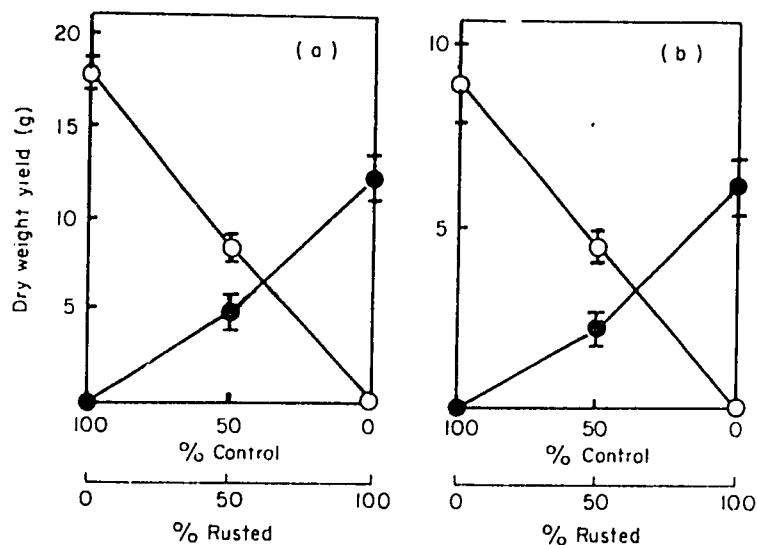


FIGURE 8. Effects of powdery mildew and drought stress on the growth of barley, and bulk water potential at different depths in the soil profile of stressed plants, 8 days after inoculation. Plants were well watered or watering was stopped on the day of inoculation (water potential of leaf 3 was for healthy -0.49 ± 0.03 and -0.95 ± 0.03 watered and stressed, respectively; for infected, -0.46 ± 0.02 and -0.91 ± 0.02 watered and stressed, respectively). Healthy, hollow bars; infected, filled bars. Each value is a mean of 6 replicates with standard error. (From Ayres, 1982.)

Effects of water stress on rusted groundsel

FIGURE 9. Replacement series diagram for (a) well watered and (b) droughted populations of (○) healthy and (●) rust (*Puccinia lagenophorae*)-infected groundsel (*Senecio vulgaris*). Relative crowding coefficient, yield of control in mixture divided by yield of rusted in mixture, all divided by yield of control in monoculture divided by yield of rusted in monoculture, was 1.06 for (a) and 1.51 for (b). (From Paul & Ayres, 1987.)



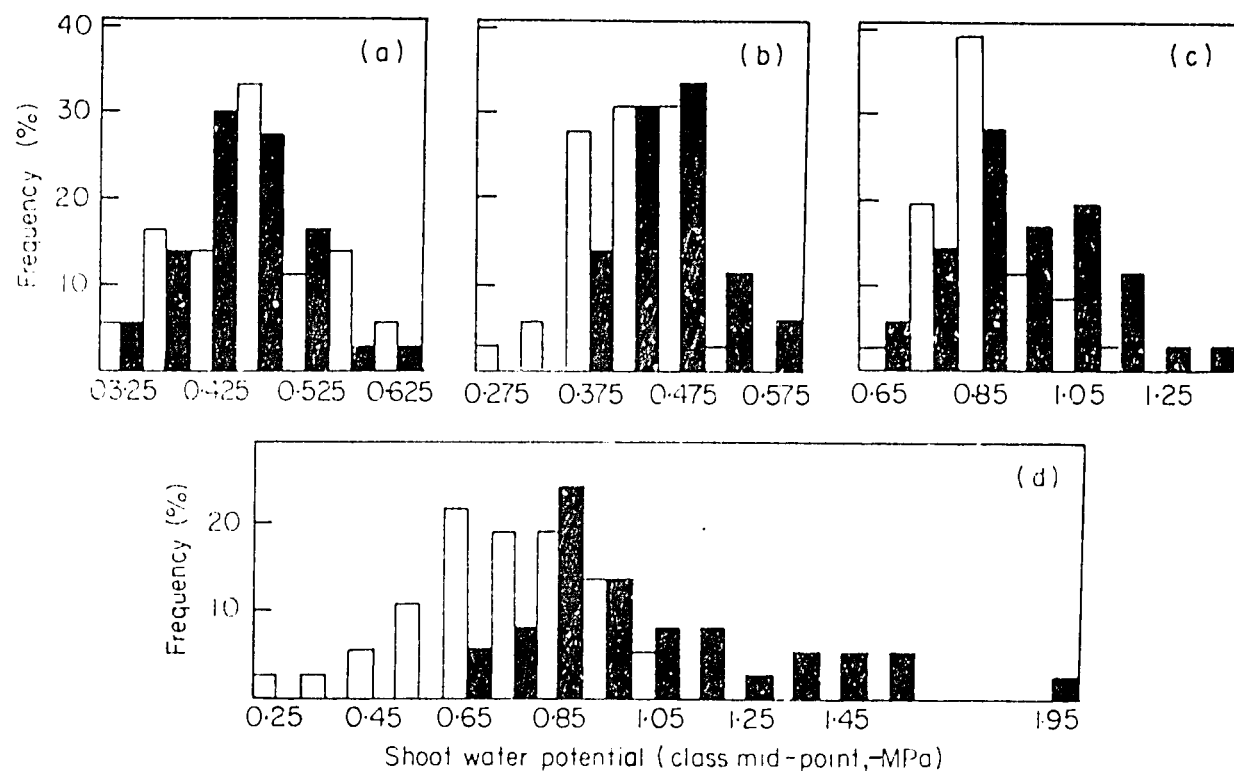


FIGURE 10. Frequency distribution of shoot water potentials of control (open bars) and rusted (solid bars) groundsel grown in (a) well watered monocultures, (b) well watered mixtures, (c) droughted monocultures, (d) droughted mixtures. (From Paul & Ayres, 1987, where full statistical analysis is given.)

Modeling Crop Response to Growth Reducing Factors

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Summary

Pests, diseases, and weeds are growth reducing factors which affect the physiology of the crop in several ways. The final effect on yield can be quantitatively understood by evaluating the effects of the respective injury components and their interactions by means of simulations with comprehensive crop growth models. This approach elucidates the integrative physiology of the "stressed" crop. Moreover, it provides new insights that suggest ways for developing simple descriptive models which can be applied in crop loss assessment and warning systems. Examples are drawn from studies on fungal leaf diseases, the viral leaf disease beet yellows virus, and aphids.

Introduction

Yields of agricultural crops vary among different agricultural regions of the world and, within those regions, from year to year and location to location. To structure thinking about this variation in yield, three yield levels can be distinguished (*Figure 1*; de Wit & Penning de Vries, 1982; Rabbinge & de Wit, 1989): (1) the *potential* level, (2) the *attainable* level, and (3) the *actual* level.

Potential yields are attained with ample supply of water, nutrients, and other resources in the absence of weeds, pests, diseases, or other injurious factors. This situation is rare and may only be obtained in protected cultivation. The potential yield depends on site-specific abiotic conditions and crop physiological characteristics. Site parameters are sunshine profile over the year and over the day, temperature, humidity, CO₂ concentration, and physical soil properties. Major crop characteristics are phenology and architecture, assimilate allocation, and physiological mechanism of CO₂ binding (C3, C4, or CAM). Together these factors can be regarded as yield defining factors. Potential growth rates are in the order of magnitude of 25 g DM (dry matter) m⁻² d⁻¹ (= 250 kg DM ha⁻¹ d⁻¹). Methods for simulating potential yields on the basis of defining factors are discussed by de Wit *et al.* (1978), Penning de

Vries and van Laar (1982), and Penning de Vries *et al.* (1989). As radiation is often the dominant limiting resource for growth under optimal conditions, the growth rate also can be roughly estimated as 3.0 (μg DM J⁻¹) times the intercepted photosynthetically active radiation, expressed in J m⁻² d⁻¹ (Biscoe & Gallagher, 1977; Monteith, 1977; Russell *et al.*, 1989; Haverkort *et al.*, 1990).

The yield level decreases to the *attainable* level when one or more resources are not provided *ad libitum*. De Wit and Penning de Vries (1982) distinguish production situations with yield limitation by shortage of water, shortage of water + nitrogen, and shortage of water + nitrogen + phosphorus. Water loss through the stomata is an inevitable consequence of the uptake of the CO₂ needed for photosynthesis, and depends on incoming radiation, vapour pressure deficit of the air, and stomatal aperture. For each gram of dry matter assimilated in photosynthesis, about 150 to 300 g of water is evaporated. Such transpiration coefficients indicate that crops transpire 4 to 8 mm water per day to attain the potential growth rate. When less water is available, the stomata close such that the rate of photosynthesis is reduced. The high rates of leaf photosynthesis needed for potential yields can only be attained at elevated nitrogen concentrations in the leaf dry matter of ±6% (van Keulen *et al.*, 1989). Assuming an LAI of 4 m² (leaf) m⁻² (ground) and a specific leaf area of 20 m² (leaf) kg⁻¹ (leaf DM), 12 g m⁻² of nitrogen would be needed only for the leaves to reach the potential growth rate. Such resource quantities of nitrogen are often not available. Shortages of resources *limits* growth rate. Of course, these calculations provide only "first" estimates. Methods for estimating crop growth under limiting availability of resources more precisely are discussed

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by van Keulen and Wolf (1986) and by Penning de Vries *et al.* (1989).

Due to pests, diseases, weeds, adverse conditions and pollutants, the attainable growth rate is seldom realized in practical agriculture. The rate of growth is *reduced* to the *actual* level. The size of the reduction depends on the ways in which the growth reducing factor affects the plant. Often a growth reducing factor has more than one effect on the plant, and the effect on final yield (damage) is the outcome of all different types of injury (injury components) and their interactions. Crop growth models can be of great help in understanding and quantifying the interactions between different injury components. This approach provides insight into the way in which and the amount by which growth is reduced in connection with growth defining and growth limiting factors and may lay a basis for simple management models (Rabbinge & Rijsdijk, 1981; Boote *et al.*, 1983; Rabbinge, 1986, 1988a,b; Rabbinge & Rossing, 1987, 1988; Rabbinge *et al.*, 1989, 1990). In this paper, some simulation studies of crop response to growth reducing factors from the Wageningen school of theoretical production ecology will be presented to illustrate the underlying principles and possible applications.

Injury Components

Damage is defined as any reduction in the quantity and/or quality of yield (Zadoks, 1985). *Injury* is any visible or measurable changes in the plant caused by a growth reducing factor. Damage can be split into components in the same way as yield. For instance, cereal aphid attack may decrease the *number* of kernels, the *weight* of kernels, and their *quality* (protein concentration). Damage is the final result of the effects of the injuries during a growing season on the physiology of the crop and the rate of growth. A growth reducing factor has seldom only one effect on the host. Often different types of injury are caused. Therefore, we can speak of *injury components*. Many effects from the molecular to the crop level can be found in the literature (Table 1). To understand the consequences of a growth reducing factor on crop growth, the effects on the physiology of the whole plant as part of the crop must be studied. On this integration level, four major functional systems can be distinguished: the economies of carbon, water, nutrients, and morphogenesis (Table 2). These systems are, of course, highly interdependent. Growth reducing factors interfere with all these systems, but most research has been conducted on the effects on

the source term of the carbon balance — photosynthesis.

Fungal Leaf Pathogens

Introduction

Many important fungal leaf diseases are initiated by air-borne spores which land on the leaf surface and cause infection. A colony of mycelium develops locally in or on the leaf, disrupting normal leaf functioning and resulting in the development of visible symptoms. The effect on gas exchange by single leaves can be described with a simple equation which can be built into a crop growth simulation model to calculate effects of different diseases on the crop. In this approach, the physiological relations between the fungus and the host plant are neglected. Details on biochemical and leaf physiological details are given by Farrar and Lewis (1987). Here, we focus on the description of the effects on the integration level of the leaf, as outlined by Bastiaans (1990).

The Relation Between Disease Severity and Leaf Photosynthesis: A Model

The percentage of leaf area covered with lesions, the severity, is a function of the number of lesions and their size according to

$$s = 1 - (1 - \alpha)^N \approx 1 - e^{-N \cdot \alpha} \quad (1)$$

Here, s is severity (proportion) and α , a small number, is lesion size expressed as a proportion of leaf size. N is the number of lesions. The equation is valid when lesions are randomly distributed over the leaf (Justesen & Tammes, 1960). The effect of the disease on photosynthesis can be described with

$$\text{fraction photosynthesis reduction} = 1 - e^{-N \cdot \alpha \cdot \beta} \quad (2)$$

where the product $\alpha \cdot \beta$ denotes the "influence area" of a lesion. In this influence area, the rate of photosynthesis is assumed to be 0 (Bastiaans, 1990). It follows that the relation between leaf photosynthesis and disease severity is given by

$$P_s = P_0 \times (1 - s)^\beta \quad (3)$$

or, establishing a linear relationship by taking logarithms

$$\ln(P_s) = \ln(P_0) + \beta \times \ln(1 - s) \quad (4)$$

where P_s is photosynthesis at severity s , P_0 is photosynthesis of a healthy leaf, and β is the ratio of the

influence area of a lesion and its visible surface. Though this description is developed from the idea of a lesion with surrounding leaf area with inhibited photosynthesis, its descriptive power also can be used in cases where such localized physiological lesions do not exist. To stress this fact, the influence area is called "virtual."

Leaf photosynthesis depends on many factors, of which incident light, ambient CO₂, and leaf water status are among the most important. The relation between photosynthesis and light is conveniently described with a negative exponential equation with three parameters (Goudriaan, 1982; Figure 2):

$$P_n = -R_d + (P_m + R_d) \cdot \left(1 - \exp\left(-\frac{\epsilon \cdot H}{P_m + R_d}\right)\right) \quad (5)$$

where

P_n = net rate of photosynthesis (= gross assimilation minus respiration)

P_m = the asymptotic maximum net photosynthesis rate at light saturation

ϵ = the initial slope of the photosynthesis-light response curve

R_d = the rate of respiration (growth respiration + maintenance respiration)

H = light intensity

Application of the β -Model

The β -model is now used to explore some published leaf injury-photosynthesis relationships. An extended version of Equation 3 (see Appendix) is used to describe relationships in which gas exchange at 100% severity deviates significantly from zero. The models were fitted to the data using the nonlinear least squares regression algorithm DUD (Ralston & Jennrich, 1979) implemented in the NLIN procedure of the SAS statistical software package.

Literature Data and Results

Rabbinge *et al.* (1985) determined the effect of mildew infection on carbon exchange parameters in winter wheat. The results with the fitted models are given in Figure 3. Parameter values are given in Table 3. In the two-parameter model, the effect on P_m is characterized by a β value of 5.8 ± 0.56 (SEM), indicating that the effect on leaf photosynthesis is significantly greater than can be explained by a loss of photosynthesis in the mildew-covered area alone. The effect of mildew on the initial slope of the photosynthesis light response curve is characterized by a β of 1.5 ± 0.37 , not significantly different from the value of 1 that would reflect the absence of photosynthesis

only in mildew-covered spots. Effects on R_d cannot be described with the two-parameter model because the function value at 100% severity deviates too much from zero.

Application of the three-parameter model to the wheat mildew data gives slightly better fits to the data. However, the accuracy of the parameter estimates, especially β , is strongly reduced. β estimates are much higher than in the two-parameter model, which indicates that the effect of the disease at low severities is greater than the two-parameter model suggests (Figure 3).

Other diseases for which leaf photosynthesis-severity relationships have been measured are wheat glume blotch (*Septoria nodorum*), wheat brown rust (*Puccinia recondita*), barley leaf blotch (*Rhynchosporium secalis*), and peanut leafspot (caused by *Cercospora* spp.). For the three cereal diseases, the effect on P_m was established (Rooney, 1989; Spitters *et al.*, 1990; Martin, 1986). For *Cercospora* leafspot disease in peanut (Boote *et al.*, 1990), photosynthesis was measured at an arbitrary (undefined) light intensity. Data and fitted models are given in Figure 4. Parameter estimates are given in Table 3. The three cereal diseases appear to have β values that do not differ significantly from 1. This implies that their impact on leaf functioning may simply be regarded as a reduction of green area and a waste of the light that is intercepted by the lesions. For wheat brown rust, the non-deviation from 1 of β is confirmed in the three-parameter model, that can allow for the occurrence of a residual respiration in leaves that are 100% rusted. *Cercospora* leaf spot in peanut has a β value of 11 ± 3.5 , indicating an effect on leaf photosynthesis that exceeds the proportion of leaf area occupied by lesions.

Sances *et al.* (1982) give an example of an injury-photosynthesis relationship for an invertebrate pest, avocado brown mite (Figure 5). As shown by the three-parameter model, the impact of mite injury is characterized by a β value not different from 1. Thus, the loss in photosynthetic rate is proportional to the leaf area injured. Injured leaves exhibit residual photosynthesis rates amounting to approximately 50% of those in healthy leaves. It is unclear whether the low photosynthesis rates given by Sances *et al.* are typical for avocado or consequences of sub-optimal conditions.

Discussion

The different β values for the effects on P_m and ϵ allow some speculations to be made on the physiological basis of the effect of mildew on wheat

photosynthesis. The large β values for the effect on P_m and the low value for the effect on ϵ are consistent with the hypothesis that closure of stomata (either homogeneously over the leaf or patchwise; Terashima *et al.*, 1988; Downton *et al.*, 1988) is a major physiological response of wheat to mildew infection. Such stomatal closure would limit photosynthesis at light saturation by decelerating the diffusion of CO_2 into the leaf. It might not have a significant effect on the photosynthesis at low light levels, as diffusion through partially closed stomata (in the case of homogeneous closure) or lateral diffusion (in the case of patchwise closure) might be sufficient to maintain the internal CO_2 -concentration at the same level as in healthy leaves.

In the different examples, the three-parameter model generally gave the best fit. The two-parameter model provided more accurate parameter estimates, however, and it has the advantage of a simpler physiological interpretation.

Beet Yellows Virus: A Viral Leaf Pathogen

Unlike most fungal leaf diseases, viruses are generally systemic, as they are transported in the phloem (Matthews, 1981). Thus, the symptoms often cover whole leaf blades, rendering the equations described in the previous section unsuitable for the description of effects on photosynthesis. A well-studied example of the effects of a viral leaf disease on photosynthesis is beet yellows virus, one of the causal agents of virus yellows, a major disease of sugarbeet worldwide.

Beet yellows virus belongs to the closterovirus group and is transmitted by aphids in the semi-persistent manner (Bar-Joseph *et al.*, 1979). The principal vector is *Myzus persicae*, the green peach aphid. Upon transmission of the virus to a plant, the virus is multiplied in the inoculated leaf. After one or a few days, the virus is transported to the growing tissues, leaves, and roots (Bennett, 1960). Symptoms develop on the inoculated leaf and on the systemically infected leaves. Mature non-inoculated leaves do not become systemically infected (van der Werf *et al.*, 1989a), presumably because there is no or negligible phloem transport of virus to these assimilate-exporting leaves. Yellowing symptoms develop after an infected leaf is fullgrown (van der Werf *et al.*, 1989b). Until these symptoms appear, the rate of photosynthesis is not markedly affected. Thus, BYV-infected plants in the Dutch climate may have three distinct whorls of leaves: (1) an inner whorl of young leaves

which are systemically infected but still green and photosynthetically active, (2) an outer whorl of healthy mature and old leaves that appeared before the plant became infected and which are photosynthetically active, and (3) an intermediate whorl of mature systemically infected leaves which are yellow and (almost) photosynthetically inactive (Hall & Loomis, 1972a,b; van der Werf, 1988).

Other viruses causing leaf yellowing symptoms in sugarbeet are beet mild yellowing virus and beet western yellows virus. Both viruses belong to the luteovirus group and are persistently transmitted by *Myzus persicae*. The effects of these viruses on the beet plant resemble those of beet yellows virus. Symptoms take somewhat longer to develop.

Models of the yield impact of these viruses are developed along two lines: (1) comprehensive, and (2) descriptive. The comprehensive modeling approach on the basis of injury components makes use of the SUCROS model, as described by Spitters *et al.* (1989a). Four injury components are quantified to calculate the effect of virus infection on the plant: (1) reduced leaf expansion, (2) increased scattering of incident light by yellow leaves, (3) reduced photosynthesis rate in yellow leaves at high and low light intensities, and (4) increased respiration in yellow leaves. These injury components were initially observed in beet yellows virus-infected plants, but are now also applied for simulating the growth of plants infected with beet mild yellowing virus.

The first injury component is presently built into the model by introducing measured leaf area indices as a forcing function (Figure 6). Injury component 2 is introduced by calculating a weighed average scattering coefficient for the whole leaf canopy on the basis of the observed proportions of green and yellow leaf area and measured scattering coefficients of 0.12 and 0.40, respectively (van der Werf, 1988). In the model, only two types of leaves are distinguished—green and yellow. For the green leaves, the leaf photosynthesis parameters of Spitters *et al.* (1989a) are used: $P_m = 1.25 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\epsilon = 12.5 \text{ } \mu\text{g CO}_2 \text{ J}^{-1}$. For yellow leaves (injury component 3), the parameter values are: $P_m = 0.28 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\epsilon = 9.7 \text{ } \mu\text{g CO}_2 \text{ J}^{-1}$. Increased respiration (injury component 4) is taken into account by assuming that yellow leaves exhibit 2.5 times higher maintenance respiration than normal healthy leaves. Details are given in van der Werf (1988).

Model predictions are compared with results of a field experiment in 1989 in which sugarbeet plants were infected with either beet yellows virus or beet

mild yellowing virus (Figure 7). The infection was made in the cotyledon stage. The model slightly underestimates the real production figures. Differences in yield among the three treatments are, however, fairly well described by the model. An earlier sensitivity analysis of the model (Rabbinge *et al.*, 1990; Table 4) showed that the reduction of photosynthetic capability of the yellow leaves is the principal injury component, explaining 70% of the yield reduction.

The descriptive model is based on the overruling importance of the reduction of photosynthesis in the yellow leaves as demonstrated by the comprehensive model. Photosynthesis in the yellow leaves is neglected. By weekly field observations with a grid, the percentage soil cover by green leaves was determined (Figure 8), and the integral of photosynthetically active radiation (PAR) intercepted on green leaves was calculated from these data and meteorological figures from a nearby weather station. In Figure 9, total biomass during the season is plotted against the cumulated PAR interception on the green leaves. Data points for the three treatments are described by production efficiencies of 1.4 to 1.7 $\mu\text{g (DM) J}^{-1}$ (intercepted PAR), indicating that this simplifying approach gives a fair first estimate of yield loss due to virus yellows, caused by beet yellows virus or beet mild yellowing virus. However, production efficiencies for beet yellows virus-infected plots seem to be lower than for control or beet mild yellowing virus-infected plants. Thus, not all the variation is explained.

Perspective

Modeling with injury components provides a tool for calculating the implications of measurements at leaf level for the crop as a whole. Thus, the gap between plant physiology and crop science is bridged. Sensitivity analyses may indicate principal injury mechanisms and the model may be used for assessing the effects of crop husbandry and virus control measures. The light interception approach seems to provide a tool for determining yield reduction at the field level.

Aphids

Aphids injure their host plants through several mechanisms (Miles, 1989a,b). The three most important are: (1) consumption of sugars, amino acids, and other phloem constituents; (2) leaf coverage with honeydew; and (3) injection of physiologically active substances, toxins, or growth regulators.

Groenendijk *et al.* (1990) simulate the effect of the black bean aphid, *Aphis fabae*, on growth of young sugarbeet plants by quantifying the withdrawal of sugars by the aphid population (Figure 10). The model assumes an assimilate requirement of aphids of 1.6 mg (sugar) mg^{-1} (aphid dry weight) d^{-1} . Photosynthesis is calculated on the basis of simulated leaf area, incident radiation, and measured photosynthesis parameters. Injury component 2 (honeydew) was not included in the model because measurements by Hurej and van der Werf (unpublished) did not demonstrate photosynthesis inhibition by honeydew. Injury component 3 was also neglected because no data demonstrating toxic effects have been published. Simulation results correspond well with actual yield data (Figure 11). This result supports the hypothesis that assimilate consumption is the most important injury component.

Sensitivity analysis of the model (unpublished) shows that the timing of infestation is crucial for the effect of the aphids on the plant. When aphid infestation is late, the sugar drain due to aphid feeding is insignificant as compared to the assimilation rate, such that the effect on daily production and leaf growth is negligible. When aphid infestation begins in an early growth phase of the plant, assimilate withdrawal constitutes a significant drain and causes a marked decrease in the daily relative growth of the plant. Thus, in an experiment in which the aphids were introduced when sugarbeet seedlings were in the two-leaf stage, the relative growth rate decreased from 0.018 d^{-1} in control plants to 0.14 d^{-1} in aphid-infested plants (Groenendijk *et al.*, 1990). Due to the positive feedback between growth and light interception, these daily growth reductions culminate in a reduction in weight from 30 to 9 g after four weeks. Thus, insight is obtained that may help in establishing economic thresholds for this aphid.

Rossing (1991a,b) simulates the effects of the cereal aphid, *Sitobion avenae*, in winter wheat, incorporating injury components 1 and 2 according to measurements of Rossing and van de Wiel (1990). He quantifies both the consumption of sugars, ca 1.6 mg (sugar) mg^{-1} (aphid dry weight) d^{-1} , and the consumption of nitrogen via the amino acids in the phloem sap: ca 30 $\mu\text{g (N) mg}^{-1}$ (aphid dry weight) d^{-1} . Consumption of sugars affects the growth of the kernels directly through reduction of the amount of assimilates available for growth. Two alternative possibilities are evaluated for the quantification of the effects of consumption of nitrogen:

(1) The aphids have priority over the kernels in the acquisition of the available nitrogen, the amount

of which does not change as compared to the aphid-free situation. Thus, the rate of kernel growth is reduced by lack of sugars and nitrogen from the onset of the aphid infestation.

(2) The nitrogen demand by the aphids accelerates the redistribution of nitrogen from leaves. Thus, kernel growth is initially not hampered; but later on, rates of growth fall below those of the aphid-free simulation because leaf senescence has been accelerated.

It is not known which of these hypotheses best reflects the real situation. Fortunately, the different hypotheses have only slight consequences for the ultimate effect of the aphids on the yield. Measured effects of honeydew on leaf photosynthesis parameters are also incorporated in the model. Based on the simulation model, a descriptive model for yield loss as a function of aphid density is derived which is as accurate as the best empirical model published in the literature. Moreover, the modeling study provides dynamic relationships between aphid load and effects on crop growth that can fine-tune existing supervised control decision rules for cereal aphid control (EPIPRE; Drenth *et al.*, 1989). Such fine-tuning is only possible with detailed dynamic simulation models.

Conclusion

This paper gives an arbitrary selection of simulation studies on pests and diseases as yield reducing factors. Methodologically similar studies were made on the air pollutant SO₂ (Kropff & Goudriaan, 1989; Kropff, 1990), groundnut rust (Savary *et al.*, 1990), and weeds (Kropff, 1988; Spitters, 1989; Spitters *et al.*, 1989b; Kropff & Spitters, 1990). Other studies are in progress. The aim of this type of work is to provide better quantitative insight concerning the effects of growth reducing factors on the physiology and production of crops in interplay with growth defining and growth limiting factors. Such insight is needed for rationalizing pesticide usage against growth reducing factors of biotic origin, such that the productivity of crops can be maintained with a minimum of side effects on the environment.

Most studies on the physiology of plant-pathogen interactions are made on the molecular and biochemical integration level (reviews in Pegg & Ayres, 1987). On the higher integration level of the whole plant, the research effort is considerably smaller. Little attention has been paid, for instance, to the relation between disease severity and leaf CO₂ exchange parameters. In only one publication (Rabbinge *et al.*,

1985) are all three parameters describing the photosynthesis response on light quantified. The other publications study the effect on only one of these parameters and therefore give insufficient background for making photosynthesis calculations for field conditions. This lack of knowledge is one of the reasons for the current practice of risk-avoiding insurance-sprays.

Simulation studies based on quantified injury components provide a crop-physiological basis for the development of practical models such as linear relationships between intercepted radiation and yield (Waggoner & Berger, 1987; Waggoner, 1990; Spitters, 1990). The β -model (§3) may describe disease-host relationships on the leaf level and provide a useful extra disease-specific parameter in these production efficiency models. β values of 1 suggest that the effect of a disease may be described with the simplest type of model, neglecting radiation intercepted on lesions, provided that the vertical disease profile is more or less homogeneous.

Acknowledgements

We thank ir Irma Jorritsma and ir Herman van Roermund for kindly providing the original data published in Rabbinge *et al.* (1985) and Spitters *et al.* (1990), and ir Rinco de Koeijer and mr Hennie de Ruiters for their share in the observations and simulations on beet yellowing viruses. Ir marcel van Oyen gave useful comments on an earlier version of this paper.

Appendix: Basis of the Three-Parameter Model

Assume a leaf with N randomly distributed lesions with visible relative size α and virtual influence area $\alpha \cdot \beta$. Photosynthesis (or another gas exchange parameter) of the healthy leaf area is P_0 and the value for the influence area is P_a . In the two-parameter model, P_a is 0. Severity is again $s = 1 - e^{-N \cdot \alpha}$ and the area in which gas exchange is affected by the disease covers again a proportion, $1 - e^{-N \cdot \alpha \cdot \beta} = 1 - (1 - s)^\beta$, of total leaf area while the healthy leaf area covers a proportion $(1 - s)^\beta$. It follows that the gas exchange, averaged over the leaf area is now:

$$P_s = P_0 \cdot (1 - s)^\beta + P_a \cdot \{1 - (1 - s)^\beta\}.$$

Thus, $P_s = P_a + (P_0 - P_a) \cdot (1 - s)^\beta$.

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TABLE 1. Effects of growth reducing organisms on plants.

Organisms	Effects
Fungi	Withdrawal of materials from the host, creation of holes in the leaf surface, increasing water loss, reduction of light absorption through mycelium development on the leaf surface, disruption of host tissue integrity by excretion of lytic enzymes, excretion of physiologically active substances acting as toxins or hormones (Williams, 1979).
Bacteria	Tissue degradation, alteration of membrane permeability, obstruction of water movement in xylem, excretion of toxins (Kelman, 1979).
Viruses	Disruption of hormonal balances, reduction of rate of photosynthesis, interference with phloem translocation of sugars, increase of rate of respiration, inhibition of leaf expansion (Matthews, 1981; van der Werf, 1988).
Leaf-eating insects	Reduction of leaf area, creation of entry ports for leaf pathogens.
Aphids	Withdrawal of sugars and amino acids, injection of physiologically active compounds with the saliva, excretion of sugary honeydew on leaf surface resulting in pathogen stimulation, sealing of stomata and coverage of leaf surface with light intercepting black moulds, reduction of rate of photosynthesis (Wood <i>et al.</i> , 1988; Miles 1989a,b; Rossing & van de Wief, 1990).
Mites	Mechanical damage due to punctures, removal of cell contents, closure of stomata due to disfunctioning of guard cells, injection of physiologically active substances with the saliva, reduction of rate of photosynthesis (Tomczyk & Kropczynska, 1985).
Nematodes	Removal of cell contents, injection of physiologically active excretions, induction of giant cells, cell wall dissolution, reduction of rate of photosynthesis, disruption of hormone production in root tips, tissue destruction, hampering uptake of water and nutrients by roots, creation of entry ports for root pathogens (Dropkin, 1979; Wallace, 1987; Melakeberhan <i>et al.</i> , 1988).

TABLE 2. Principal processes in plants which can be affected by growth reducing factors.

PROCESSES	GROWTH REDUCING FACTORS
CARBON AND ENERGY ECONOMY	
Photosynthesis Light interception & distribution CO ₂ diffusion CO ₂ binding Other chloroplast processes	Weeds, necrotrophic fungi Many fungal & viral leaf pathogens
Respiration Maintenance New syntheses (growth) Photorespiration	Many fungal & viral leaf pathogens Leaf diseases
Allocation Transport	
WATER ECONOMY	
Uptake Transport	Root pathogens, nematodes Vascular wilt diseases (<i>Verticillium</i> , <i>Fusarium</i>)
Transpiration, stomatal regulation	Leaf diseases
NUTRIENT ECONOMY	
Uptake Transport Redistribution	Root pathogens, nematodes Vascular wilt diseases (<i>Verticillium</i> , <i>Fusarium</i>) Leaf diseases
MORPHOGENESIS	
Organ initiation Organ growth	Mycoplasmas, galling aphids Most growth reducing agents (per def.)

TABLE 3. Characterization of published relations between diseased (injured) leaf area & leaf photosynthesis rate w/the β -model.

Leaf area disease	Parameter	Two- (one-) parameter model			Three-parameter model				n
		P_0^*	β	R^2	P_0^*	P_a^{**}	β	R^2	
Wheat powdery mildew ¹	P_m (mg CO ₂ m ⁻² s ⁻¹)	1.11 ± 0.021	5.8 ± 0.56	0.63	1.17 ± 0.022	0.56 ± 0.045	25.0 ± 4.8	0.73	95
	ϵ (µg CO ₂ J ⁻¹)	7.4 ± 0.14	1.5 ± 0.37	0.23	7.6 ± 0.1 ^c	6.0 ± 0.48	19.0 ± 13.1	0.28	64
	R_d (mg CO ₂ m ⁻² s ⁻¹)	not applied			0.036 ± 0.013	0.049 ± 0.0026	25.0 ± 12.4	0.34	76
Wheat glume blotch ²	P_m (proportion)	1 (fixed)	1.66 ± 0.34	0.55	not applied				14
Wheat brown rust ³	P_m (mg CO ₂ m ⁻² s ⁻¹)	0.51 ± 0.020	1.26 ± 0.16	0.77	0.51 ± 0.020	-0.08 ± 0.066	0.95 ± 0.24	0.78	68
Barley leaf blotch ⁴	P_m (proportion)	1 (fixed)	2.1 ± 0.61	0.68	not applied				12
Peanut leafspot ⁵	P_n (proportion)	0.92 ± 0.10	11.0 ± 3.5	0.88	0.99 ± 0.058	0.25 ± 0.056	27.0 ± 8.3	0.98	5
Avocado brown mite ⁶	P_n (mg CO ₂ m ⁻² s ⁻¹)	not applied			0.21 ± 0.020	0.10 ± 0.014	1.3 ± 0.7	0.96	4

* P_0 is the photosynthesis parameter at severity 0; ** P_a is the parameter value at 100% severity.

¹*Erysiphe graminis* (Rabbinge *et al.*, 1985), ²*Septoria nodorum* (Rooney, 1989), ³*Puccinia recondita* (Spitters *et al.*, 1990);

⁴*Rhynchosporium secalis* (Martin, 1986); ⁵*Cercospora* spp. (Boote *et al.*, 1980), ⁶*Oligonychus punicea* (Sances *et al.*, 1982).

TABLE 4. Simulated relative contribution of components of injury by beet yellows virus in sugarbeet field experiment, 1986.

Damage components	Early infection		Late infection	
	Yield (%)	% damage*	Yield (%)	% damage*
No disease	100.0		100.0	
		7.1		1.5
1 (reduced leaf area index)	92.9		98.5	
		5.2		0.2
1+2 (reduced light absorption)	88.0		98.2	
		36.4		1.7
1+2+3 (reduced photosyn. ϵ , A_m)	56.0		96.6	
		11.7		0.5
1+2+3+4 (increased respiration)	49.4		96.1	
Measured	48.2 \pm 2.5		93.4 \pm 5.1	

*% damage is the damage (%) calculated by incorporating the injury components one-by-one in the model:

Early infection: June 5, 1986 7 leaves LAI = 0.1

Late infection: July 17, 1986 21 leaves LAI = 5.1

More details are given in van der Werf (1988) and in Rabbinge *et al.* (1990).

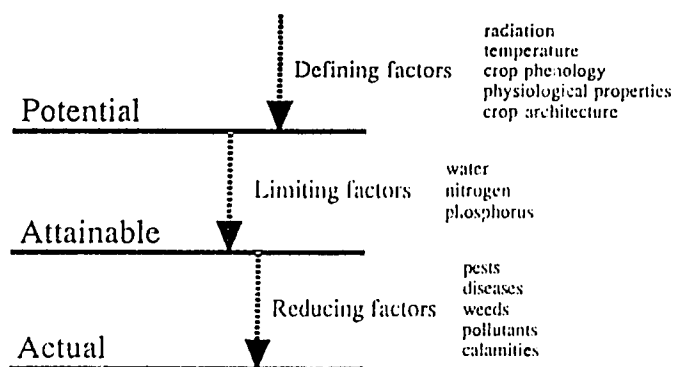
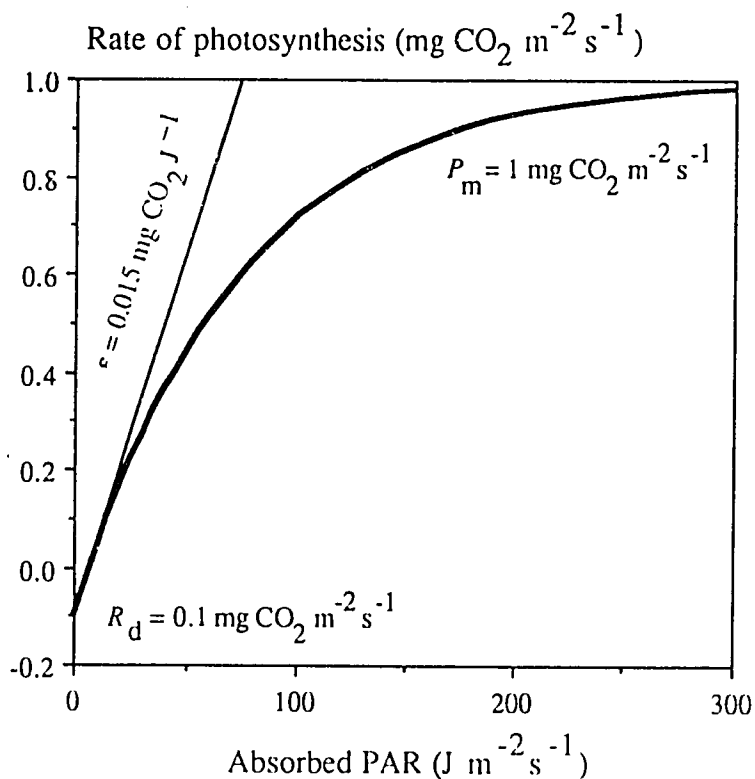
**FIGURE 1.** Crop production levels.**FIGURE 2.** Negative exponential equation for describing the photosynthesis light response curve of leaves (Equation 5).

FIGURE 3. Photosynthesis parameters of winter wheat leaves as affected by infection with powdery mildew, *Erysiphe graminis*. (Data from: Rabbinge *et al.*, 1985.)

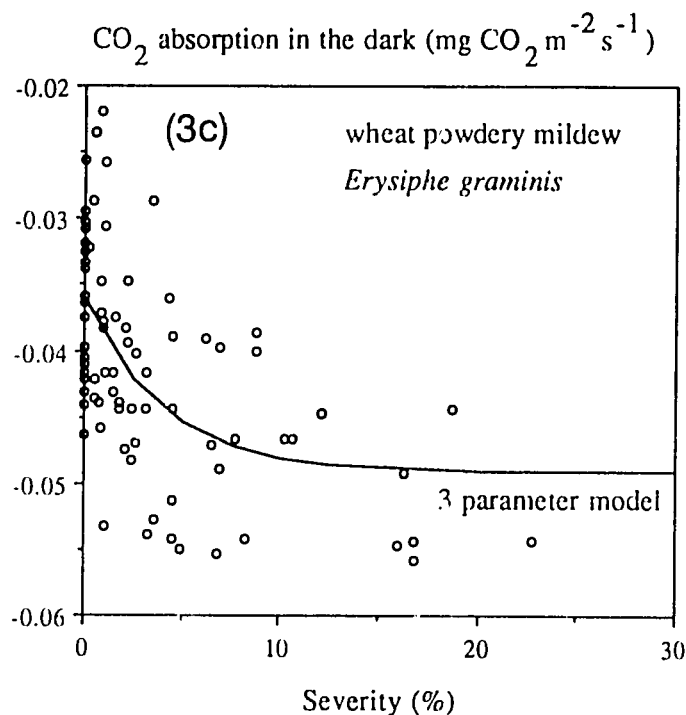
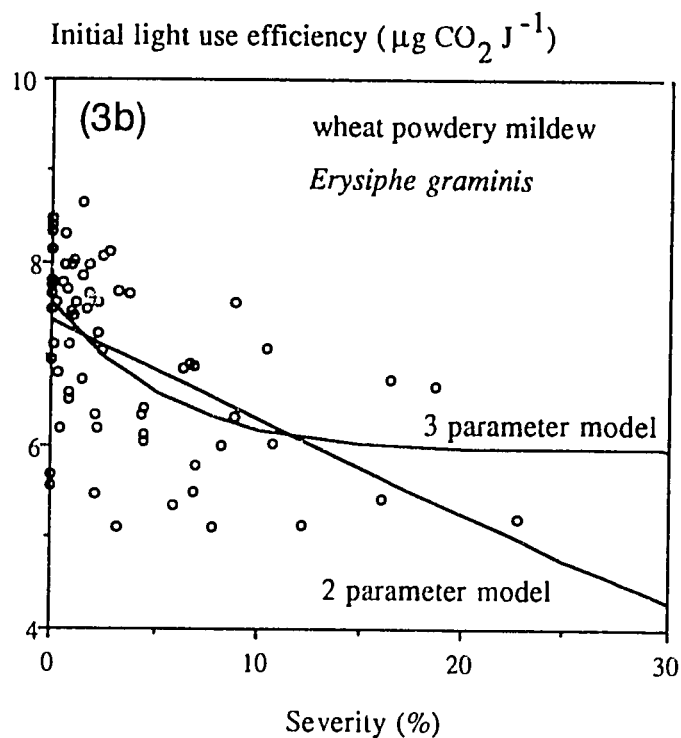
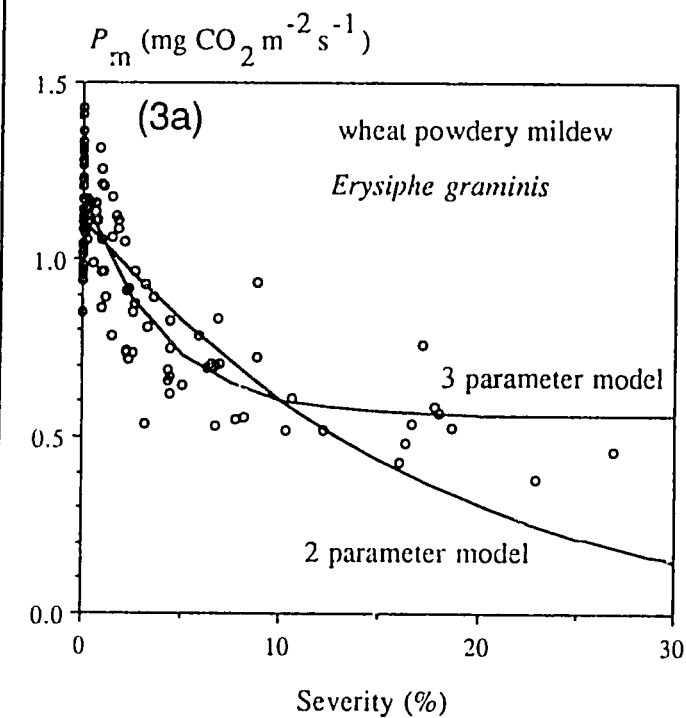
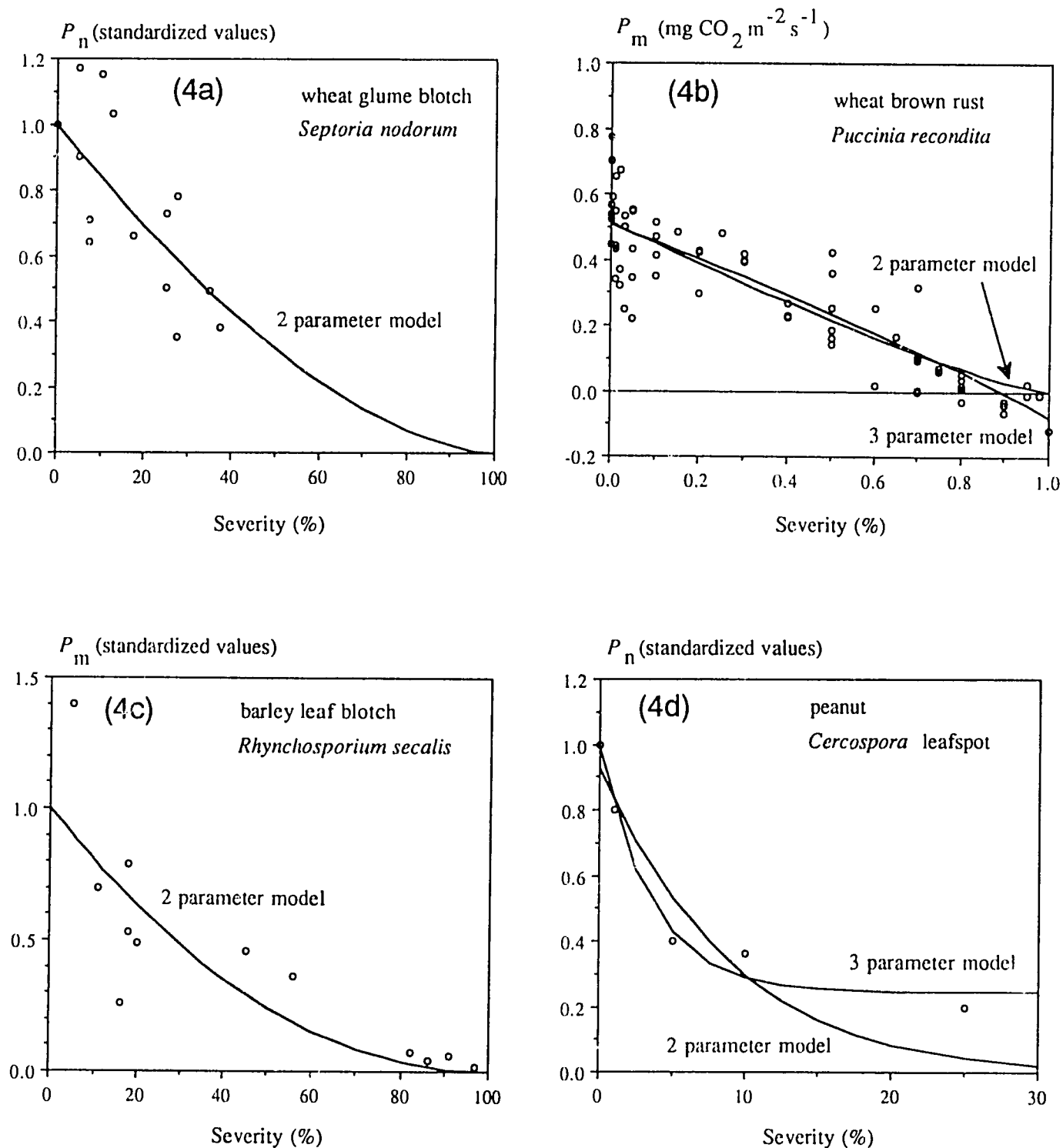


FIGURE 4. Leaf photosynthesis as affected by infection with foliar pathogens in four patho-systems: wheat glume blotch, *Septoria nodorum* (data from Rooney, 1989); wheat brown rust, *Puccinia recondita* (data from Spitters *et al.*, 1990); barley leaf blotch, *Rhynchosporium secalis* (data from Martin, 1986); and peanut leafspot, *Cercospora* spp. (data from Boote *et al.*, 1980).



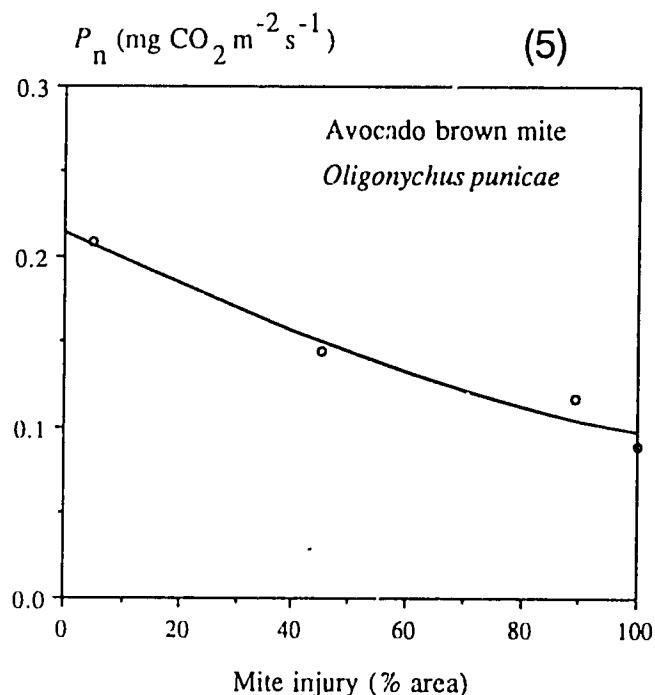


FIGURE 5. Leaf photosynthesis in avocado as affected by feeding injury by avocado brown mite, *Oligonychus punicae*. (Data from Sances *et al.*, 1982.)

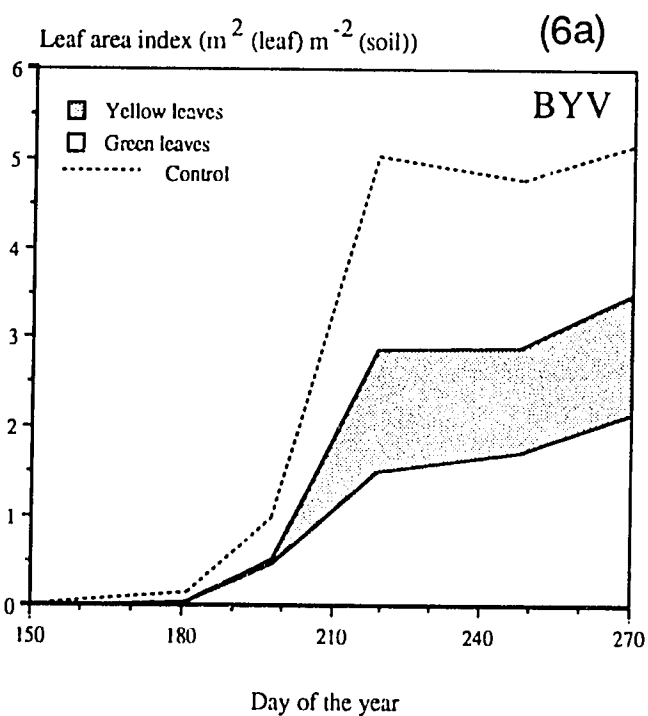


FIGURE 6. Observed course of leaf area index in sugarbeet field experiment, 1989.

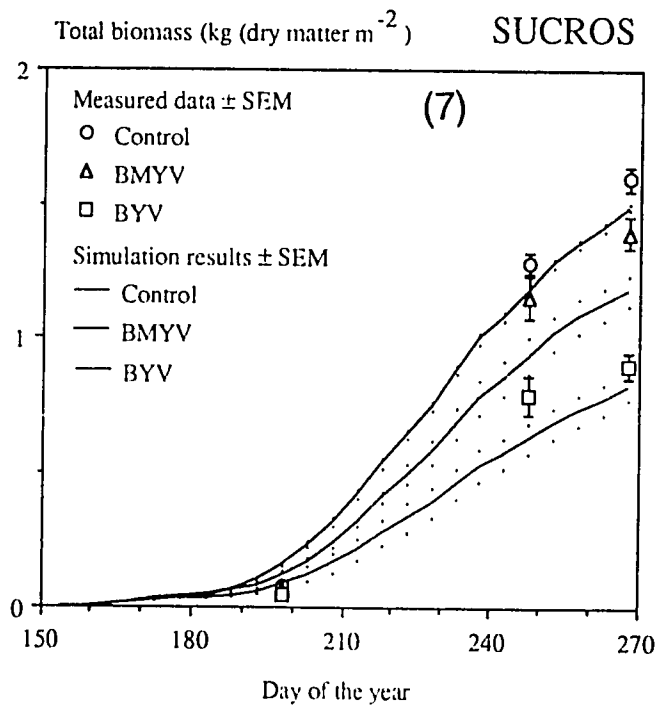
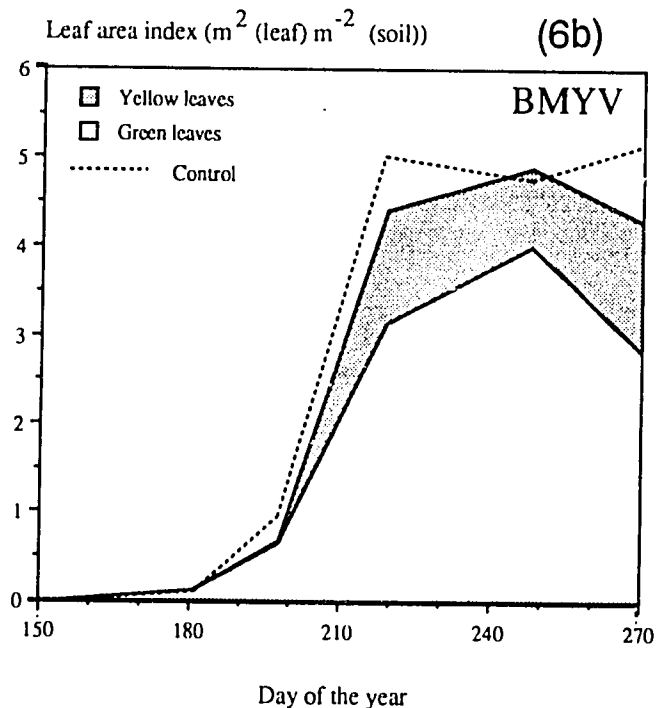


FIGURE 7. Comparison of observed sugarbeet growth in 1989 with calculations by the comprehensive model SUCROS. The standard error of the simulation results (indicated by dots) was obtained by running the model with LAI data from single experimental plots.

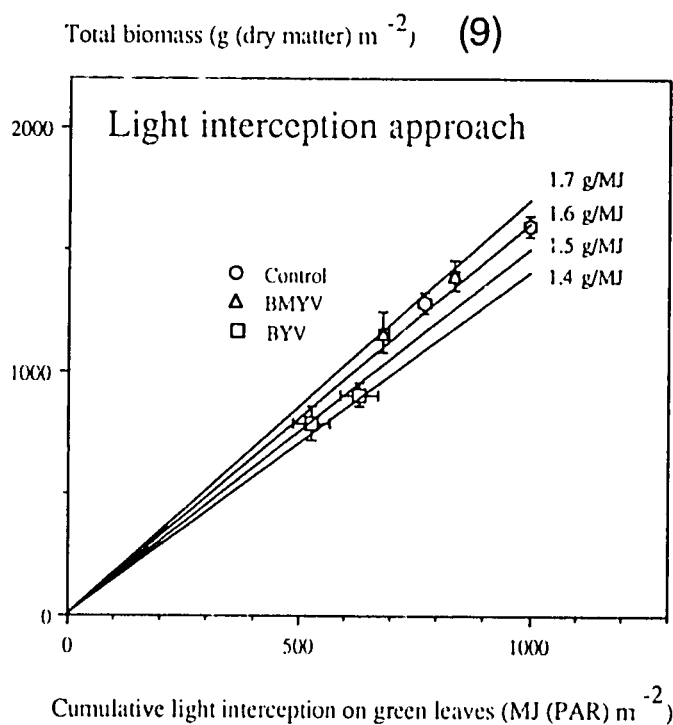
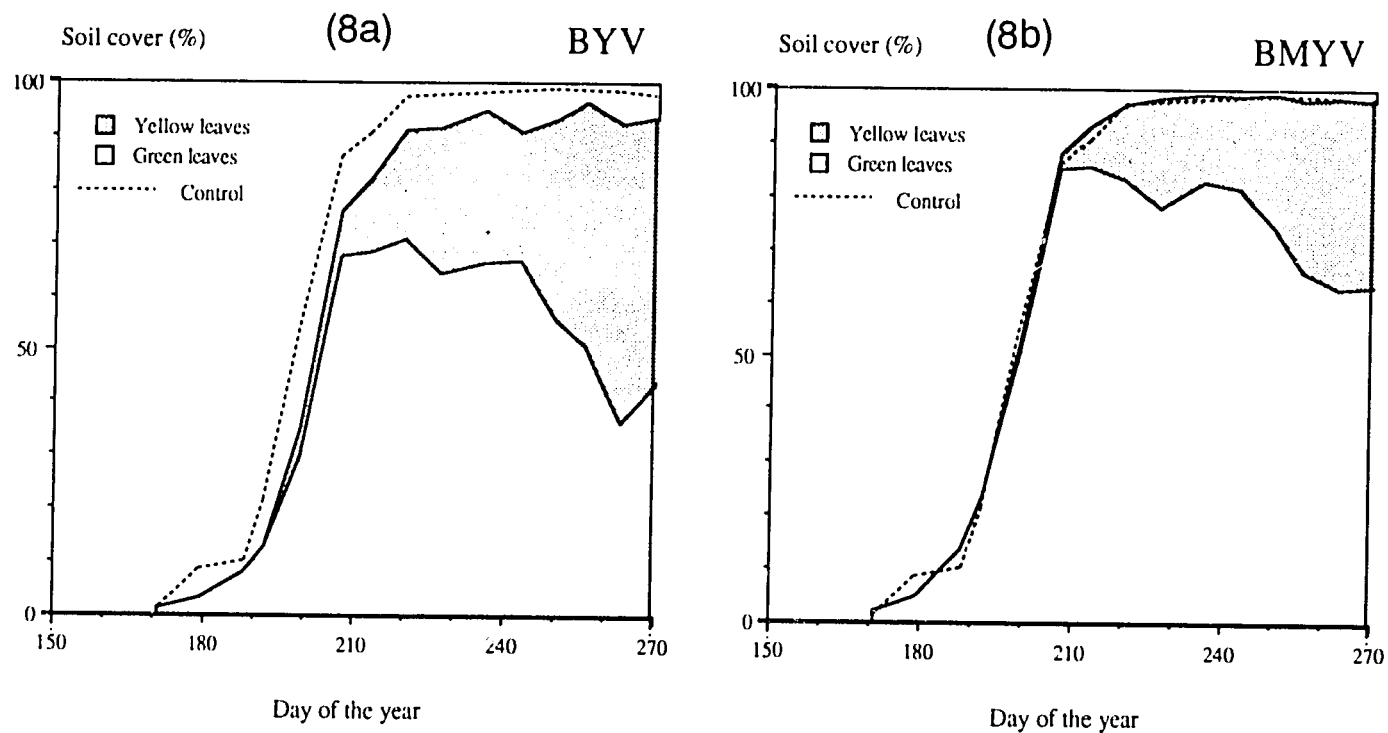
FIGURE 8. Observed course of soil cover in sugarbeet field experiment, 1989.**FIGURE 9.** Observed relation between cumulative interception of photosynthetically active radiation (PAR) by green leaves and production in sugarbeet field experiment, 1989.

FIGURE 10. Structural diagram of sugarbeet-aphid damage-model. (Data from Groenendijk *et al.*, 1990.)

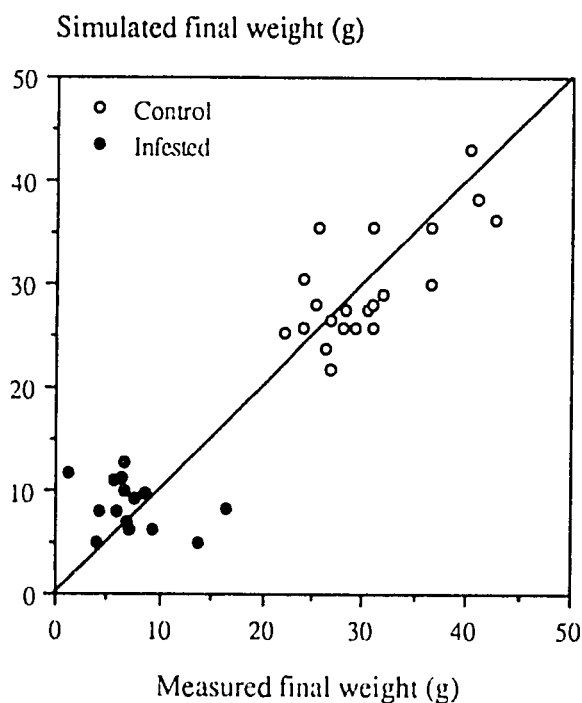
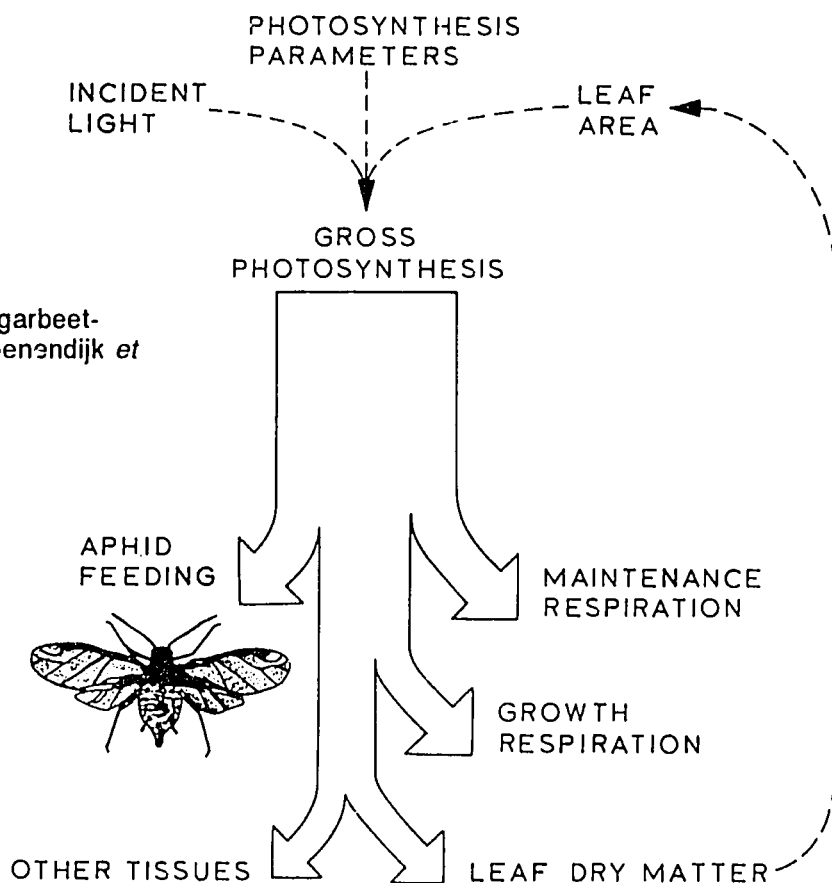


FIGURE 11. Simulated versus measured final dry weight of uninfested and aphid-infested sugarbeet plants, four weeks after infestation with *Aphis fabae* at the cotyledon growth stage. (Data from Groenendijk *et al.*, 1990.)

Influence of Mycorrhizae on Barley in Arid Environments

William E. Grey*

Introduction

Roots support the growth of a complex of soil-borne fungi that can have an effect on plant growth. The majority of plants growing under natural conditions are dual organisms in that the organs through which they absorb water and nutrients consist of root and fungus tissue. These fungus-roots are called mycorrhizae and constitute the most widespread root infections of plants.

Mycorrhizae can be divided into two organs based on anatomical characteristics. The ectomycorrhizae, which occur mainly in woody plants, form a sheath around the root and penetrate and grow between cortical cells. The endomycorrhizae, including the vesicular-arbuscular mycorrhizae (VAM), penetrate the living cells within roots. The VAM fungi are most important in agricultural crops and infect most angiosperms, including the grasses.

Mycorrhizae develop when a hypha from a spore or an already infected root contacts a root hair, develops an appressorium on the epidermis behind the meristematic region, and forms a network of inter- and intracellular hyphae within the cortex (Hayman, 1983). VAM penetrate a parenchyma cell to form an arbuscule without killing the root cell or modifying the external root morphology. Dichotomous branching of the arbuscule hyphae are enveloped by a host-derived encasement layer and the continuously invaginating host-plasmalemma. The close contact between arbuscule and parenchyma cell ensures a high exchange surface for transport of carbon compounds and mineral nutrients. Individual parenchyma with arbuscules are connected to one another with intercellular hyphae and with extramatrical hyphae that radiate into the rhizosphere. Vesicles containing lipid bodies function as food storage organs or as reproductive organs if they develop into thick walled chlamydospores. VAM fungi survive as mycelium in infected plant roots or as soil-borne chlamydospores. Currently, the chlamydospore cell wall morphology and structure are criteria for identification of VAM fungi (Schenck & Perez, 1988).

The VAM fungi, being obligate parasites, depend on the photosynthetic capacity of their plant host for

carbon compounds. The host plant benefits primarily by an extension of the absorption surface of its roots resulting in an increased uptake capacity for mineral nutrients and water (Hayman, 1983). In general, plants with an extensive root system such as the grasses are less dependent upon a mycorrhizal association to extract nutrients and water from the soil. However, the facilitation of phosphate uptake, due to its poor mobility in the soil, is particularly stimulated by the presence of VAM. The growth responses of mycorrhizal plants in phosphate deficient soils is a major reason for the attention given to the VAM.

VAM and Their Importance in Barley

Phosphate uptake in an annual crop may only be significantly affected if VAM are established shortly after seedling emergence (Jakobsen & Nielsen, 1983). A beneficial growth response may occur if 10% of the seedling root is colonized and accompanied with a well developed external mycelium (Sanders *et al.*, 1977). In temperate climates, fall sown cereals may have substantial levels of infection during the autumn (Hetrick & Bloom, 1984). However, this early infection may undergo a decline in the proportion of the colonized mycorrhizal roots during the winter (Dodd & Jeffries, 1986, 1989). In North America, the peak infection in winter wheat is late spring and early summer before root senescence because of early season low soil temperatures (Hetrick *et al.*, 1984). Spring sown wheat and barley also experience a delay in root infection when planted early, but there is a rapid increase with rising temperature in summer (Black & Tinker, 1979; Buwalda *et al.*, 1985). Root colonization studies on winter cereals sown early in the fall and on rate of development of infection in spring cereals would suggest that soil temperature may be a limiting factor in establishment of mycorrhizal roots in temperate climates.

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VAM fungi, which are most effective at increasing the growth of annual plant species, infect rapidly and extensively (Abbott & Robson, 1982). Barley growth responses are often associated with high mycorrhizal colonization in low but not deficient soil phosphate (Jensen, 1982). In addition, minor element uptake by mycorrhizal roots can overcome nutrient deficiencies. Inoculation of barley with VAM fungi at the time of planting in the field with available soil phosphate doubled the weight of heads (Clark & Mosse, 1981). The addition of phosphate with one of the VAM inoculants further increased yield by 35%. However, high levels of easily available phosphate have a negative effect on VAM colonization (Black & Tinker, 1979). In field surveys of Danish agricultural soils, there is often a reduced intensity of infection by indigenous VAM fungi with high phosphate, but the shoot-phosphate level was the same in low and high fertility plots. This would suggest that nutrient levels are unimportant to infection and that reduced soil-phosphate levels are balanced by a higher mycorrhizal infection and greater efficiency of phosphate uptake (Jensen & Jakobsen, 1980). It is probable that fungal species and strains exist that are adapted to levels of soil nutrients.

VAM fungi may increase the drought resistance of host plants by either maintaining growth under stress, speeding recovery from wilting, or in providing a more efficient use of water (Sieverding, 1986). Mycorrhizal plants have reportedly improved grain yields under stressed conditions in wheat (Ellis *et al.*, 1985), but not in maize and sorghum (Simpson & Daft, 1990). Benefits from VAM infection under drought conditions may depend on root and water distribution in the soil and the duration of any period in water stress (Simpson & Daft, 1990).

VAM fungi exhibit physiological adaptation to the environment. VAM fungal isolates from tropical climates had a higher optimum germination temperature than those from temperate climates. Differences in optimum temperatures for mycorrhizal colonization among *Glomus* spp. have been reported in wheat (Hetrick & Bloom, 1984). Optimum infection of winter wheat with *G. epigaeum* occurred at 25°C but not at 10°C. Beneficial plant growth responses to mycorrhizal colonization are temperature dependent and may even be reduced as compared with nonmycorrhizal plants due to low temperature stress (Clarke & Mosse, 1981). However, the benefits from early root colonization in the spring may be an advantage to plants that are not normally colonized until later in the season, such as cereals.

Co-adaptation of Host and Endophyte

Most plants form a highly specialized mycorrhizal association that is not specific and will often host a range of fungal species that act as mycorrhizae (Molina *et al.*, 1978). Also, the wide range of VAM fungi found in naturally formed ecosystems suggests that a diversity of fungal species have adapted to similar ecological factors (Schenck & Kinloch, 1980). In contrast, monoculture crops have acted selectively on indigenous endophytes and have reduced the diversity in an agriculture soil. Co-adaptation of an annual crop, such as barley, and spore forming VAM endophytes in agricultural soils to environmental stress may have selected for superior host and endophyte combinations.

Barley was one of the first domesticated crops in the Fertile Crescent of Syria and Jordan (Ceccarelli *et al.*, 1987). Stress such as drought, cold, heat, and salinity are common in these environments. Syrian barley landraces or selections from landraces are widely grown and are considered dependable by farmers for high yields, especially where environmental stress is the yield-limiting factor. In the semi-arid conditions of North America, barley has been developed for high yield and yield stability over a multitude of environments. The hypothesis that co-adaptation of host and endophyte has selected for superior combinations was tested by Grey (1991) utilizing barley selected from Syrian landraces, barley adapted to semi-arid conditions in Montana, and the associated VAM fungi collected from Syrian and Montana agricultural soils. These would seem to represent a host-endophyte association from relatively recent agriculture in Montana to an association that could be traced back to the domestication of barley from *Hordeum spontaneum* in the Fertile Crescent of Syria and Jordan (Harlan, 1979).

Temperatures can have an effect on early mycorrhizal colonization of barley (Grey, 1991). It was found that mycorrhizae from Syria and Montana developed at a range of temperatures from 11 to 26°C, but a greater proportion of colonized roots occurred at warm temperatures. In addition, in soils at 26°C, a growth stimulation was associated with an increased proportion of the root colonized by mycorrhizae. VAM fungi from Montana, primarily *Glomus macrocarpum*, were more tolerant of cool soils of 11°C, whereas VAM fungi from Syria, primarily *G. hoi*, were more tolerant of warm soils of 26°C. The proportion and intensity of mycorrhiza after infection had occurred was similar between the VAM from

Syria and Montana at warm temperatures of 17°C. However, in a cool soil, the proportion of colonized root was greater with VAM fungi from Montana than from Syria. In an environment with sudden rises in temperature, colonization rate may be more important to the success of a host and endophyte association than the minimum required temperature for infection. Soil temperatures are warmer in Syria when barley is sown in the fall and during regrowth in the spring than in Montana when barley is planted in the spring. A beneficial growth response by the host would require rapid colonization of the seedling by heat tolerant VAM fungi in Syria and cold tolerant VAM fungi in Montana.

VAM fungi are obligate parasites, but there is no case of a single fungal strain restricted to a particular host plant. Grey (1991) also reported no specific reaction between the barleys adapted to Syria or Montana and the associated VAM fungi from these regions. However, it was possible to distinguish genotypes for the presence of a mycorrhiza provided the soil temperature was favorable for the adaptation of VAM isolate. For instance, VAM fungi from Montana distinguished genotypes in cool and temperate soils but not in warm soil. On the other hand, VAM fungi from Syria distinguished genotypes in warm and temperate soils but not in the cool soil. Furthermore, a lower number of infectious propagules was required for detection of a mycorrhiza when utilizing a barley cultivar adapted to Syria ("Harmal") than from Montana ("Clark"). Formation of a mycorrhiza may contribute to the stability of barley in a stressed environment.

Summary

The importance of VAM will largely depend upon the agricultural inputs. Under conditions of high moisture or high fertility, there may be no effect by VAM on plant growth. Under low inputs, or periods of fluctuations in plant stress, a mycorrhizal plant may also have no change in growth response. The maintenance of a stable growth response during periods of crop stress rather than enhanced growth may be the significant contribution of VAM.

The selection for mycorrhizae in a plant breeding program would need to address the role of mycorrhizal colonization and efficiency (Grey, 1991). Mycorrhizal colonization is a measure of the reaction between host and endophyte, whereas efficiency is a comparison of growth response with a noninfested plant (Menge, 1983). Barley genotypes could be screened for ability to form extensive mycorrhiza with

minimal inoculum of indigenous soil VAM fungi. An efficient host-endophyte combination could be selected based on a stimulated growth response in the glasshouse or yield stability in field trials. The deployment of cultivars with high mycorrhizal colonization and an efficient mycorrhiza may contribute to yield stability under a variable stress environment.

Studies on the benefit of mycorrhizae to agriculture have emphasized the identification of species or strains with desired characteristics and the exploitation of those strains as inoculants (Abbott & Robson, 1982; Hetrick *et al.*, 1984; Menge, 1983). However, the major problems of VAM inoculum production and dissemination must first be addressed before this goal is met (Baltruschat, 1987). Utilization of barley genotypes with ability for mycorrhizal colonization may favor the natural selection of VAM fungi with increased spore production, rapid colonization of roots, and stimulated growth responses in the host.

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Effects of Stress on the Etiology of Barley Yellow Dwarf Virus

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Summary

Moderate drought is often accompanied by an increase in barley yellow virus (BYDV) damage. The stressed plants produce a higher proportion of alates, which increases the rate of spread by epidemics. In natural drought conditions, the yield losses caused by BYDV were increased, especially on poor quality soils. Artificial inoculation trials proved that a factor other than the increased rate of virus spread acted to increase damage when both BYDV and drought were present. In trials under hydroponic conditions, the first virus damage in barley occurred in the root system. This specific vulnerability of the root system to BYDV could be the principal factor reducing drought resistance. The interaction between the drought and BYDV stresses produced very severe symptoms which were not necessarily typical of BYDV. Winter-kill of winter barley is also highly increased by BYDV. It is concluded that BYDV damage could often be misdiagnosed as physical or chemical stress, when both the virus and the other stress are present. In moderate drought situations the presence or absence of BYDV should be monitored with ELISA, as proper interpretation of the damage is impossible without a non-controversial assessment of virus levels.

Drought and Aphid Migrations

BYDV is a disease that can create a vicious circle that accelerates its spread. The virus disturbs the amino acid balance of plants (Ajayi, 1986), and these amino acids control the rate of reproduction of aphids (Montllor & Gildow, 1986; Markkula & Laurema, 1964) as well as the percent alates (Gildow, 1980, 1983). The end result is generally a higher biomass of aphids with a higher proportion of alates as time goes by. Although these general rules seem to hold true, it is not easy to predict BYDV epidemics, and attempts to do so met with considerable problems (Morgan, 1990). One problem with predictive models is that migrations play an important role, and these events are notoriously difficult to foresee. Even the presence of large alate populations and winds in the right direction do not guarantee that aphids will reach their next destination. In

1988, drought-induced migrations covered only very short distances in the St. Lawrence Valley area because the heat and drought were excessive for these small insects. In more favorable circumstances, the aphids can travel over a hundred kilometers in a single stretch, as the aphids coming out of winter cereals in Ontario often show up in Quebec spring cereals (Paliwal & Comeau, 1984). The worst scenario for damage in Canada occurs when the crops located in neighboring southern states have had enough moisture in early season to build up a good biomass, but then midseason drought forces the alate aphids out of the southern crop a few weeks earlier than normal. If the winds blow from the south or southwest, we are then bound to have serious BYDV infection. This pattern was observed by C.C. Gill in Winnipeg in the 70's, but the same model applied for Ontario and Quebec (Comeau, personal observations). The same kind of conditions prevailed in California in 1951, in the year of epidemic that led to the discovery of the disease (Bruehl, 1961). In summary, moderate drought after grass or cereal crops are well established can definitely be viewed as an occasion for increased spread of BYDV, although epidemics remain difficult to predict.

Etiology of BYDV Damage in Barley Symptoms on Aerial Parts

BYDV attacks all species of small grains but causes more visible symptoms in oats and barley. The delay between artificial infection and symptom appearance was significantly longer in barley than in oats (Comeau, 1987), and as the season advanced, the symptoms produced became less typical of virus infection but rather similar to the effects of natural or drought-induced plant senescence. This led to the hypothesis that BYDV epidemics could easily go unnoticed, when massive migrations of aphids occurred between Zadoks 35 and Zadoks 50, leading to

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rapid increase in BYDV infection without the typical symptoms. To verify this, large plots were infected about Zadoks 30-33. This led to visible but short-lived symptoms which showed up just before normal-looking but premature leaf senescence. This brief flurry of symptoms was accompanied by significant damage, ranging from 15 to 25% (Comeau, unpublished). Therefore, we concluded that there is a variable visibility window for BYDV symptoms in barley, and the duration of this window depends on the plant growth stage at which viral infection occurred. In artificial inoculation trials, inoculation is generally done on very young plants to facilitate the identification of resistant lines (Figure 1).

In natural BYDV epidemics in Quebec, which occurred in 1976, 1986, and 1990, it was concluded that aphid migrations were related to the observed disease levels. These intense migrations occurred during the stem elongation stages, at a time when only short-lived symptoms can be expected in barley but significant damage can still occur (Comeau, 1987). Field observations during the unusual drought year of 1988 raised new questions. In these hot, dry conditions, observations on artificially BYDV-infected lines of cereals revealed damage levels far superior to what was observed in the 16 previous years of field testing. In years of normal rainfall, BYDV inoculation of barley at the 4-leaf stage (Zadoks 14) resulted in yields of 4000 to 9000 kg/ha for tolerant lines and 1500 to 2500 kg/ha for sensitive lines. In the 1988 trials, the BYDV-tolerant lines had yield levels under infection ranging from 1848 to 4663 kg/ha, which compared to yields of 64 to 460 kg/ha for the sensitive checks (Comeau & St. Pierre, 1988). The 2-row lines were as a rule more damaged than the 6-row lines, which is understandable as the 6-row were earlier in maturity and therefore escaped part of the drought and virus damage. Some sensitive check plants had a fragile root system, so they were easily uprooted. To summarize the field data from 1972 to 1987, under artificial BYDV inoculation conditions, in normal rainfall years, the sensitive barleys yielded on average 31% of the yield of tolerant (Yd₂) barleys. Under similar artificial BYDV inoculation conditions, in the drought year of 1988, the sensitive barleys yielded only 11% of the yield of tolerant barleys. The question raised, therefore, was whether the first and principal cause of yield loss might be virus damage to the root system.

Symptoms In Barley Roots

In field epidemics observed from 1971 to 1989, the level of damage resulting from late infection

seemed to depend on the general health status of the plant. Damage was always worse on poor quality soils. In this respect, it is important to remember that healthy roots are of paramount importance to plant health, and especially so under stress conditions (Taylor & Nguyen, 1987). Roots are one of the key sites of BYDV infection. This was convincingly shown for oats (Eweida *et al.*, 1988) and maize (Henry, 1990). In our own trials on barley, the relative amount of virus detected by ELISA in barley roots varied considerably between trials. In some cases, the roots contained more virus than aerial parts, but the opposite also occurred (data not shown). We are still conducting studies on this subject.

The damaging effect of virus on the roots of oats and barley was quite striking under mist culture conditions (Kainz & Hendrix, 1981). We felt the ecological significance of these findings had been grossly underestimated, so we decided to invest some effort in the verification of this earlier report, and confirmed that the effects of BYDV on the root system of barley was indeed more dramatic than the effect on aerial parts (Haber & Comeau, 1990). In 1990, two supplementary trials were conducted. The first compared barley cultivars with or without the Yd₂ resistance gene (Schaller *et al.*, 1964). The second compared BYDV-tolerant and BYDV-sensitive barley lines to lines belonging to other species including bread wheat, durum wheat, and triticale. The tolerance levels of these lines were previously known (Comeau & St. Pierre, 1988). Plants initially grown in tubes were virus-infected at about the 2-3 leaf stage, and aphids were killed after two days. Check plants were kept virus-free. After the roots were washed, the plants were transferred to a hydroponic system similar to that described by MacKey (1973), and fed automatically with nutrient solution every 45 minutes, which caused no drought stress whatsoever. It was easy to measure the length of aerial parts of roots many times per week, and to obtain the final fresh and dry weight of these organs. Experimental variability in root growth trials was lower than expected, so that significant data could be easily obtained with two or preferably three repetitions (Tables 1 & 2).

In the first trial, BYDV infection virtually stopped the growth of the roots of sensitive cultivars, and had some minor growth-delaying effect on the roots of resistant cultivars (Figure 2). There was little difference between cultivars except that imputable to the Yd₂ gene (Table 1). In the same trial, resistant and susceptible cultivars displayed only subtle differences

in the length of aerial parts. In fact, the comparison with the virus-free check was necessary to understand which line was resistant (*Figure 1*), and the difference attributed to Yd₂ was not significant after 33 days (*Table 1*). Resistance is therefore much easier to see at the root level. The resistance observed was far from immunity but, in theory, some of the damage observed on Yd₂ lines could be attributed to the brief period of aphid feeding or to the pesticide. In the second trial, the barley lines behaved much as in the previous trial (*Figure 3*). The bread wheat lines, known to differ in field tolerance, did not show distinct growth differences in their root systems within the duration of this trial. However, the triticale line, selected for its high level of tolerance which made it far superior to any bread wheat, behaved more or less as the BYDV-resistant barleys, showing root growth despite BYDV infection. It was remarkable that the trait most responsive to virus was root length; the response of aerial parts was not statistically significant during the course of this brief experiment (*Table 2*). BYDV probably should be considered first as a root disease rather than as a disease of aerial parts. The above observations are not from the field conditions; nevertheless, they do prove that BYDV has a major and rapid effect on the root system of sensitive barley lines. Indeed, BYDV would prevent deep root penetration, depriving the plants from a most effective component of drought resistance (Blum, 1988). Rapid root elongation rates are important in seedling establishment and persistence, especially when prolonged drought occurs after seeding (Taylor & Nguyen, 1987). The effect of virus on roots would largely explain the devastating BYDV × drought interactions that we observed under field conditions in 1988. However, the effect of virus on older plants could differ from what was seen on plantlets, so that further research on the effects of BYDV under these stress conditions is warranted.

BYDV Symptoms and Mineral Deficiencies

It comes as a logical consequence that plants suffering root damage from BYDV could suffer mineral deficiencies. The poor absorption of minerals by BYDV-infected oats was previously shown (Comeau & Barnett, 1979). Among the barley lines grown in Quebec, the cultivar Chapais was outstanding for its tolerance to acid soils. Somehow this same cultivar was less damaged by BYDV in natural BYDV epidemics, although artificial inoculations showed very clearly that it did not possess the Yd₂ gene. Even under

artificial BYDV inoculation conditions, cultivar Chapais was one of the two most tolerant lines within those that did not possess Yd₂, out of 30 candidates for cultivar registration in 1987-89. The fact could be considered as an anecdote if it were not for the fact that many wheat lines from Brazil possess simultaneously BYDV tolerance and acid soil tolerance, and that triticale and rye (which are more BYDV-tolerant than wheat) are also more tolerant to acid soils. The accumulation of so-called coincidences leads one to speculate as to whether tolerance of the root system to poor soil conditions could be *ipso facto* a trait increasing virus tolerance.

BYDV and Cold Hardiness of Winter Barley

In Missouri, the mortality of winter barley was increased 11 to 27% by the action of BYDV (Grafton *et al.*, 1982). In comparable trials in Quebec, the mortality of virus-free winter barley was generally below 25% for a trial involving 46 lines from the Guelph University project, whereas the virus-infected counterpart had mortality levels ranging from 20 to 95% with an average of 48% (*Figure 4*). This trial is typical of results obtained for many years with winter barley, showing that virus infection can be more lethal than the winter cold. As the Quebec winter is much more severe than the Missouri winter, we therefore conclude that a more severe physical stress increases the severity of the effect of BYDV, so that the total stress becomes greater than the sum of the individual stresses.

In the above trials, within the BYDV-inoculated group, although one BYDV-tolerant line (OH 77-7) had high mortality (70%), all lines displaying less than 25% mortality had remarkably low BYDV symptoms. These lines — namely WB 158-1, WB 168-2, WB 180-3, WB 181-1, and WB 181-9 — might possess the Yd₂ gene, although this has yet to be proven. A more recent introduction, cultivar Wysor (from Virginia Polytechnical Institute), displays the best BYDV resistance in Quebec, and survives winter quite well. We conclude that BYDV resistance is a clear-cut asset for winter survival; it is hard to understand why breeders have not spent more effort on this trait in winter barley.

Conclusions

The first visible effects of BYDV were observed at the root level, and the effects on aerial parts may be consequences of the initial damage to the root system. Besides reducing root growth, the virus

makes the crowns and roots more susceptible to physical stress and disease (Comeau & Jedlinski, 1990), so the mechanisms contributing to damage from BYDV are complex, dependent on the environment and variable between years. Breeding for BYDV resistance has often been equated with trying to include Yd₂ in cultivars. This need not be the only approach, as lines without Yd₂ (such as Chapais spring barley) have shown satisfactory field tolerance, and as aphid and virus resistance could be obtained in the future from alien sources (Weibull, 1987). It is believed that improved root system characteristics could result from selection using artificial BYDV inoculation; the hypothesis would deserve a serious trial.

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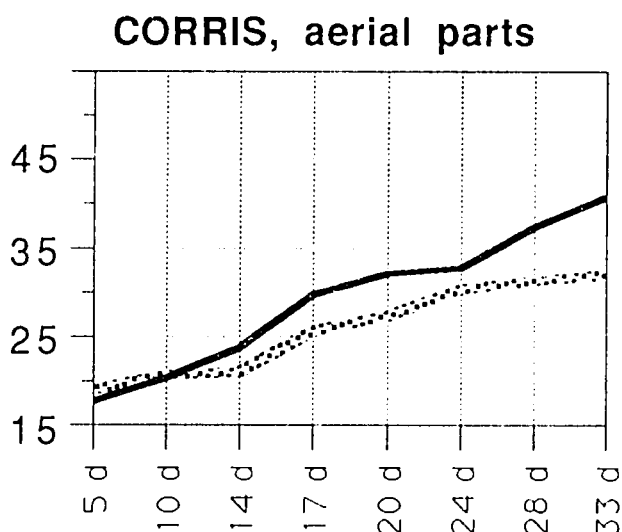
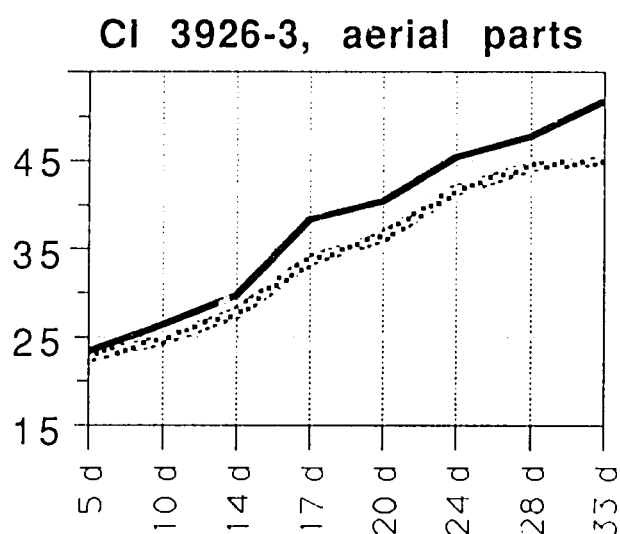
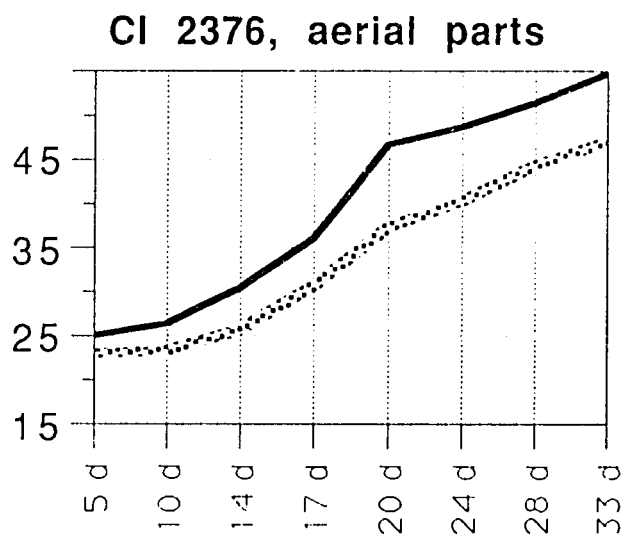
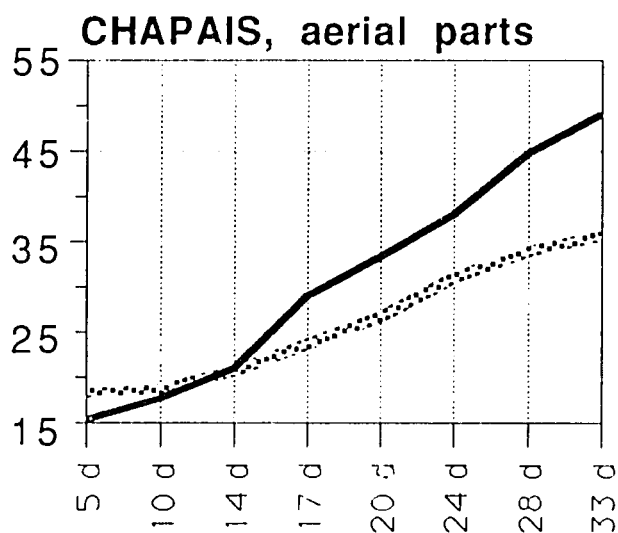
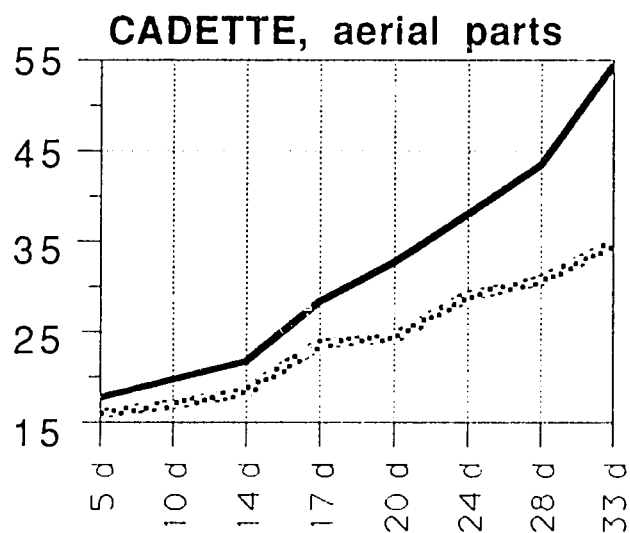
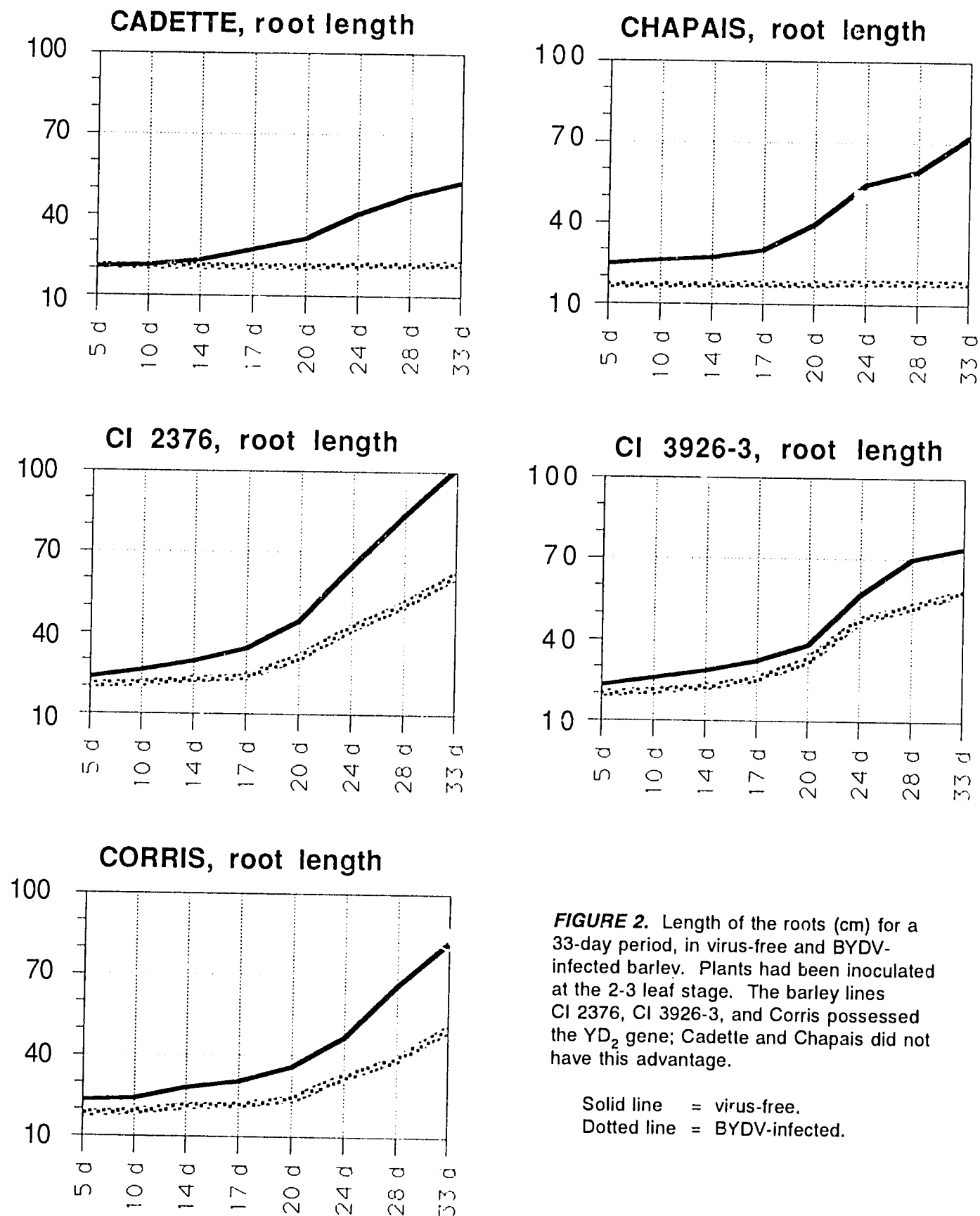


FIGURE 1. Length of the aerial parts (cm) for a 33-day period, in virus-free and BYDV-infected barley. Plants had been inoculated at the 2-3 leaf stage. The barley lines CI 2376, CI 3926-3, and Corris had the Yd₂ gene; Cadette and Chapais did not.

Solid line = virus-free.
Dotted line = BYDV-infected.



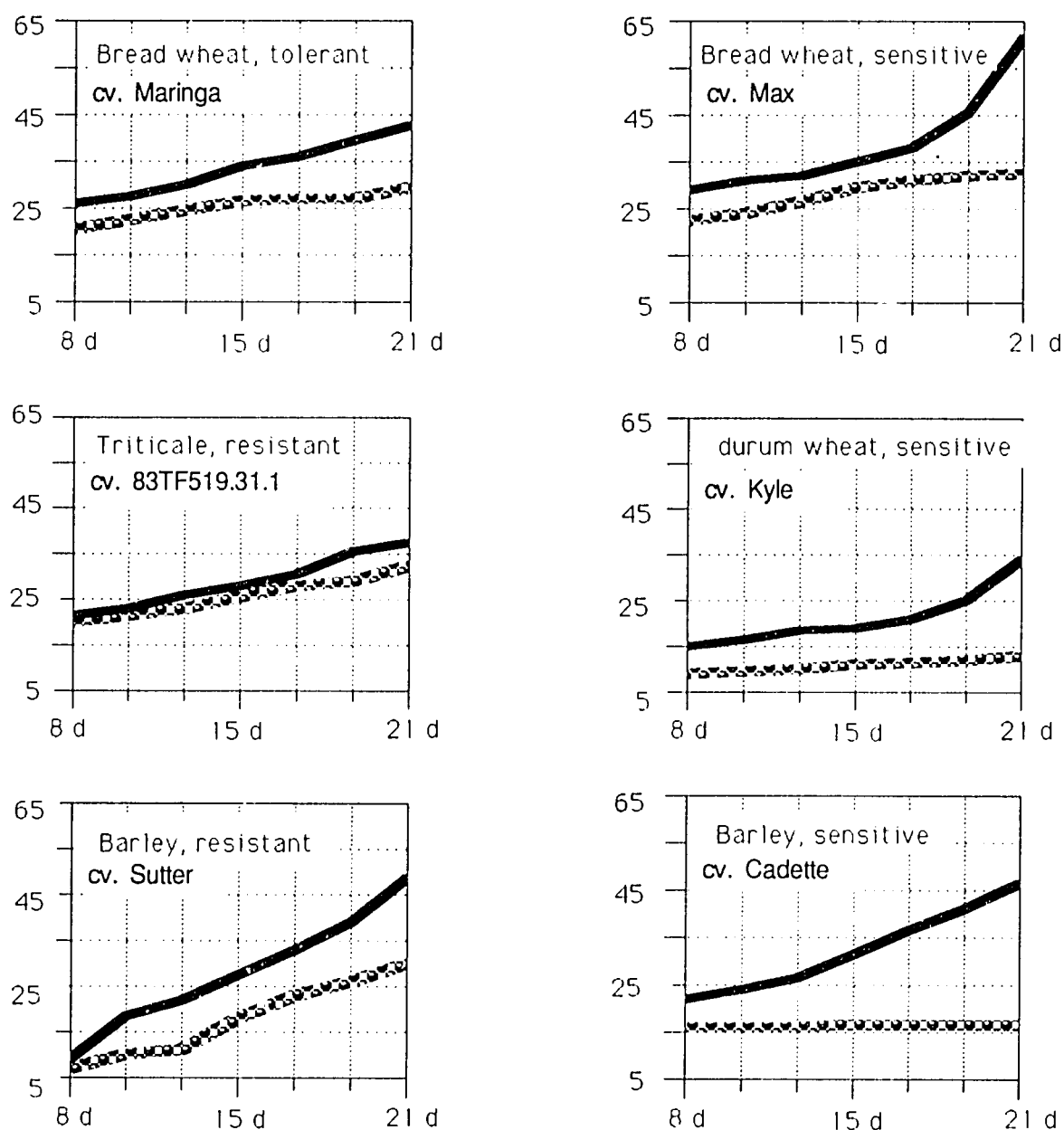


FIGURE 3. Growth or healthy (upper curve) and BYDV-infected (lower curve) roots for virus-resistant and virus-sensitive lines of many species of cereals in hydroponic conditions, up to 21 days after BYDV treatment time. The root length is expressed in cm. Solid line = virus-free; dotted line = with BYDV.

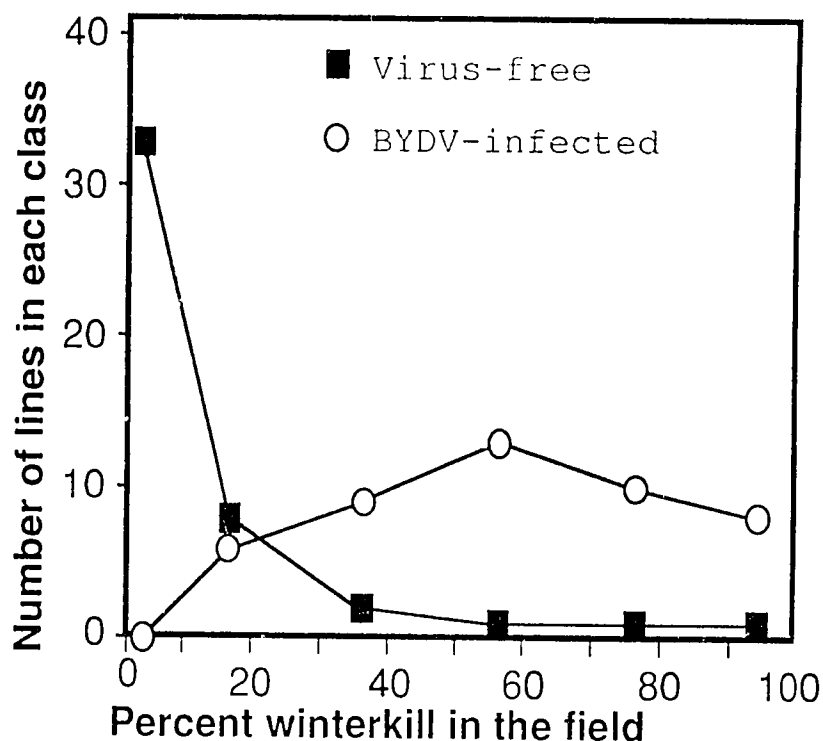


FIGURE 4. Number of lines surviving in 1985-86, within a cultivar evaluation trial involving a virus-free group and a virus-inoculated group grown next to each other in a site near Quebec City.

TABLE 1. F-values and probability levels in the analysis of variance of the first trial using hydroponic culture, on barley lines.*

Character	SOURCE	
	Yd ₂ gene	Virus treatment
Root length after 20 days	10.4 (P < 0.0034)	33.9 (P < 0.00001)
Root length after 33 days	39.1 (P < 0.00001)	53.3 (P < 0.00001)
Length, aerial parts, 20th day	13.9 (P < 0.001)	11.8 (P < 0.002)
Length, aerial parts, 33rd day	N.S.	15.7 (P < 0.0005)

*The trial involved 2 treatments (BYDV or no virus), on 5 cultivars differing in virus resistance, with 3 replicates of one plant each. The plants had spent 10 days in soil and 33 days in hydroponic conditions.

TABLE 2. F-values and probability levels in the analysis of variance of the second trial using hydroponic culture, on many species of cereals.*

Character	SOURCE	
	Cultivar	Virus treatment
Root length	2.63 (P < 0.047)	46.25 (P < 0.00001)
Dry weight, roots	2.75 (P < 0.039)	16.65 (P < 0.0007)
Dry weight, aerial parts	4.96 (P < 0.0029)	0.49 (P < 0.4902)

*The trial involved 2 treatments (BYDV at 2-leaf stage, or no virus), on species differing in virus resistance, with two replicates of one plant each. The plants had spent 12 days in soil before virus treatment and then 22 days in hydroponic conditions.

Classical vs. Recurrent Selection Breeding Approaches for Developing Disease Resistance

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For ecological as well as economical reasons, the incorporation of disease resistance or tolerance into new cultivars will be a substantial component of future breeding programs. The breeding methods to be used will be determined by many factors, including materials available to the breeder, technologies that can be applied by the breeder, and the personality of the breeder.

Disease resistance or tolerance may be of several kinds. Four types of resistance to powdery mildew in barley were discussed by Jorgensen (1987). In the first type, resistance to specific races is conferred by major genes in which host-pathogen interactions conform to the gene-for-gene system. This type of resistance has most often been used in breeding programs. Stevens (1942) recognized the role of plant breeding in aggravating crop losses due to diseases. Plant breeders that rely on major-gene resistance are victims of their accomplishments, as the popularity of a new variety results in growing large areas of a single genotype. Pure stands of the same host genotype solicit selection of mutations for new, more virulent genotypes of the pathogen. Breeding for major-gene resistance has become an unrelenting search for new sources of resistance and it ensures employment of future generations of plant breeders and plant pathologists.

Horizontal resistance, also called minor gene resistance, race non-specific resistance, field resistance, rate-reducing resistance, or partial resistance, is a quantitative character governed by additive gene action. It reduces the severity of the disease, irrespective of the genotype of the pathogen. Although horizontal resistance is more durable than major-gene resistance, it is used less in breeding programs, primarily because it is more difficult to identify and select resistant plants at the seedling stage. E.L. Sharp and his associates (Sharp, 1968; Sharp & Volin, 1970; Sharp *et al.*, 1976; Krupinsky & Sharp, 1978, 1979; Sharp & Fuchs, 1982; Reinhold *et al.*, 1983) have published extensively on minor-genes with additive effects that condition resistance to stripe rust in wheat. High levels of partial resistance to

powdery mildew in barley have been reported (Jones & Davies, 1985; Heun, 1987; Knudsen *et al.*, 1987).

Race non-specific resistance may be conditioned by single genes which do not conform to the gene-for-gene system. This type of resistance appears to be effective against most races of a pathogen. Recessive alleles at the *ml-o* locus confer resistance to powdery mildew (Wiberg, 1973) and the dominant allele at the *T* locus confers resistance to many races of stem rust in barley (Andrews, 1956).

Non-host resistance is resistance to forms or species of the pathogen that attack other host species, e.g., barley is resistant to all sub-species of *Erysiphe graminis* except those that are incited by *sp. hordei*. This type of resistance could be valuable if appropriate recombinant DNA technologies are developed to transfer genes from other host species to barley and if the genes are expressed in barley.

All four types of resistance have some characteristics in common and cannot be unambiguously separated from one another (Jorgensen, 1987).

There are many approaches to practical plant breeding and every breeder uses his own modifications of breeding methods and procedures. Classical methods and procedures, such as backcross and pedigree schemes, have traditionally been used to breed self-pollinated species. Haploid breeding, reviewed by Choo *et al.* (1985), is considered to be a form of pedigree breeding. Recurrent selection is a term originally applied to a breeding method described by Sprague and Brimhall (1950) and has traditionally been associated with breeding cross-pollinated species. Male sterility allows the use of recurrent selection techniques to breed self-pollinated crops (Ramage, 1977a, 1977b, 1980). Recently developed technologies, such as the use of restriction fragment length polymorphism to assign genes to chromosome segments and recombinant DNA methodologies to translocate the segments, promise powerful adjuncts to any breeding method.

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Certain concepts need to be considered before choosing a breeding method. Some considerations germane to selecting appropriate breeding methods and procedures to use in developing disease resistance cultivars will be discussed.

A breeder can breed for resistance to stress or for performance under stress conditions. Stress resistance is the ability to survive and reproduce, to complete a life cycle, under stressful conditions. Stress resistance is usually negatively correlated with the ability to perform under more moderate stress.

A salt tolerant population of barley was developed by male sterile facilitated recurrent selection (Ramage, 1987). Selections from the population were tested under irrigation with ocean water (Epstein & Norlyn, 1977) and yielded 1200 to 1500 kg/ha. The selections were also tested under irrigation with low-salt water and yielded only 58 to 66% (3890 to 4410 kg/ha) of the check cultivar (Ramage, unpublished). Although the lines were salt tolerant, as they were able to complete their life cycle under extreme stress, they did not perform well under less stressful conditions. Norlyn (1980) presented information that suggests that the ability of barley to yield under salt stress is heritable and that its genetic control appears to be fairly complex.

The development of charcoal rot on a cytoplasmic male sterile line and its maintainer line in sorghum (Voigt, 1967) provides an absurd analogy to illustrate the difference between breeding for resistance to stress and breeding for performance under stress conditions. A cytoplasmic male sterile that was bagged to prevent seed set did not develop charcoal rot, while its maintainer (isogenic line) was completely susceptible. Partial seed set on the male sterile line resulted in intermediate development of the disease. The absurd inference from these observations would be to breed for resistance to charcoal rot by selecting for no grain production.

Breeding for resistance to stress is not the same as breeding for performance under stress conditions. Entirely different genetic systems and background genotypes will be required for the most favorable expression of the two circumstances. Different breeding and selection techniques will be required to achieve the different objectives. Perhaps plant breeders should not breed for stress resistance; rather, they should breed material that will yield under stress conditions.

One of the basic tenets of genetics is that every character of every living organism is the product of an interaction between a specific genotype and a

specific environment. Background genotype is a large component of any environment.

Every character or combination of characters has a background genotype that is most favorable for the expression of that character or combination of characters. The phenotype of a plant is the result of all the genes of the plant interacting with each other and with the specific environment in which it is being grown. A successful cultivar is one that has a genotype balanced to accommodate the particular genetic characters of that cultivar (Ramage, 1977a). For some characters, appropriate background genotype may be just as necessary for its most favorable expression as the genotype of the character itself.

The ml-o locus for powdery mildew resistance in barley provides an example of background genotype modifying negative pleiotropic effects of a gene. Alleles at the ml-o locus provide resistance that is monogenic and non-race specific but are nearly always associated with decreased yield. Schwarzbach (1976) tested 5 ml-o mutants and their maternal varieties and reported differences in yield due to effects of the mother genotype. Kjaer *et al.* (1990) and Bjornstad and Aastveit (1990) used doubled haploid lines to demonstrate that genetic background significantly modified the negative pleiotropic effects of ml-o mutants. All concluded that by modifying background genotype, high-yielding cultivars with ml-o resistance could be developed.

Successful plant breeding is the selection of superior genotypes from a heterogeneous or heterozygous source and can be divided into two distinct phases: generation of variation and exploitation of the variation.

Generation of variation entails choosing parents and procedures to use in crosses. Crosses are made to create variability through recombination. They can be planned so that the progeny will be homogeneous for certain traits and variable for other traits, or they can be made with the principal intention of creating variability. The types of crosses made will be determined by breeding objectives. In maintenance breeding programs where the objective is to produce cultivars similar to those in current use, crosses are made to preserve previous genetic advances while providing an opportunity for improvement in other traits. Crossing to create as much variability as possible is practiced in recurrent selection programs designed to produce novel germplasm, especially when simultaneous selection for a character and its most favorable background genotype is being carried out (Ramage, 1987).

Procedures used to exploit variation differ little among breeding methods. In general, they involve selecting plants from a heterozygous or heterogeneous source, growing their progenies in plant rows, selecting among rows, and then selecting plants within the rows, growing progenies from selected plants, and repeating this sequence until relative homozygosity is reached. Selected lines are then evaluated and increased for possible release as cultivars.

Most small grain breeding programs are committed to maintaining and improving a particular background genotype such as malting and brewing quality, milling and baking quality, or local adaptation. Maintenance breeding programs are designed to produce, as quickly as possible, improved cultivars that are similar to those in current use. In such programs, yield is less important than background genotype. Almost all of the yield increases attributable to plant breeding in the last 100 years have come from stabilizing yields through introducing resistance to biotic and abiotic stresses and by increasing harvest index.

The backcross breeding method relies on selecting a suitable recurrent parent. It is usually a cultivar that is in current use, that meets user demands, and that can be improved by the addition of one or a few genes, quite often genes for disease resistance. The method involves repeated backcrossing to transfer one or a few genes from the nonrecurrent parent to the recurrent parent. Backcrossing has not been widely used (Briggs & Allard, 1953). Probably the main reasons that breeders have not adopted backcrossing are a reluctance to choose a recurrent parent and because backcrossing is not well suited for handling several characters simultaneously or for dealing with quantitative characters. A survey of the cultivars recently released in the United States indicates that one or more backcrosses are often used to obtain parents for pedigree breeding programs. This procedure, referred to as preadaptating, is used to introduce exotic germplasm, usually disease resistance, into a cultivar with specific adaptation or quality characteristics.

Pedigree breeding and pedigree method are terms used in a number of contexts and usually describe both generation of variation and exploitation of variation. Pedigree methods depend, for generation of variation, on the prudent selection of two parents that, between them, contain the characters desired in a new cultivar. In pedigree programs, crossing to simply create variability is usually not profitable. Difficulty has been experienced in finding

many useful progeny if one or both parents is ill-adapted (Briggs, 1978). To exploit the variation, rigorous selection for the characters is practiced in the segregating generations.

In generating variability, Eslick and Hockett (1974) suggested selecting parents with similar genetic backgrounds that differ in specific traits to try to retain, in the new cultivar, nebulous characters such as malting and brewing quality. Selecting parents with similar genetic backgrounds tends to preserve previous genetic advances while allowing for improvement in agronomic suitability. This approach is often used in improving agronomic productivity while retaining specific genetic backgrounds and is comparable to a backcross program for agronomic characters.

Eslick (1977) considered the typical pedigree breeding program in the midwestern United States over the last 75 years to be "a slowed recurrent selection program necessitated by the requirement of the retention of a complex of 6-row malting quality factors present in the old introduced Manchuria varieties." McProud (1979) examined cycles of selection in the pedigree breeding programs for barley in North Dakota, Japan, and The Netherlands since the early 1900's, and concluded that they were equivalent to recurrent selection programs. He separated the North Dakota program into 11 cycles averaging 6.5 years each, the Japan program into 7 cycles averaging 10.5 years each, and The Netherlands program into 7 cycles averaging 9.75 years each. Most pedigree breeding programs, along with their modifications, may be considered recurrent selection programs where selection is practiced in a variable number of generations between cycles of intercrossing.

Population breeding is a term used to describe many very diverse breeding programs. Toward the end of the nineteenth and the beginning of the twentieth century, controlled crosses between specific parents were made in many crops. Different ideologies were developed for breeding cross-pollinated and self-pollinated crops. As the science of plant breeding evolved, methods used to breed one type were adapted to breed the other type until distinctions based on mode of pollination are no longer valid. Unfortunately, ambiguity of terminology still confounds discussion of plant breeding methodology.

Recurrent selection describes breeding procedures, based on successive cycles of selection and recombination of the selections, designed to accumulate or concentrate genes for a particular quantitative

character in a population without a significant loss of genetic variability. Much of the original philosophy of recurrent selection was concerned with improving inbred lines of maize (cf. Jensen, 1988), and, traditionally, recurrent selection has been associated with breeding for yield in cross-pollinated crops.

As described by Sprague and Brimhall (1950), a typical recurrent selection program in maize involves evaluating a series of individual plants for a given character, truncating the frequency distribution at some desired level, and intercrossing the individuals comprising the truncated tail. This recombination would then serve as a source material for a new cycle of selection. Cycles would be repeated for as long as there is improvement for the selected character. The population would then be exploited by selecting plants that would be inbred to produce lines to use in hybrids, synthetic varieties, composites, etc. This typical recurrent selection program is based on several suppositions, i.e., genetic variation for the selected character is limited to that contained in the beginning base population, a cycle of selection will be reached where there is no longer significant improvement for the selected character, and a population will be developed, exploited, and then discarded.

Recurrent selection will be most effective in breeding for characters whose expression can be modified as a result of changing the background genotype, transgressive segregation, or accumulation of minor genes. In many instances, the character expression of a gene or genes can be modified strikingly by changing the genetic background of the gene. Transgressive segregants are individuals that show a more extreme development of a character than was present in the parental material and are assumed to be due to cumulative and complementary effects of genes contributed by the original parents. The accumulation of minor genes for a character is a kind of transgressive segregation (cf. Ramage, 1987).

Modern plant breeding began about 100 years ago with the development of procedures for selecting pure lines from landraces and, later, planned crosses. Breeding and selection systems that evolved were called the "bulk population breeding method" (cf. Jensen, 1988). Concepts of bulk population breeding were extended by combining a number of single crosses in various ways into one large mixture, called a "composite cross." Concerns over which genotypes are eliminated by natural selection led to studies of survival in cultivar mixtures and bulk hybrid populations. Conclusions from competition studies effected a divergence of concepts of population breeding: bulk

population breeding as an alternative to pedigree breeding for perpetuating early generations from a cross as opposed to composite cross-breeding to generate and maintain novel germplasm. The concepts of composite cross-breeding were later projected by Suneson (1956) to encompass "an evolutionary plant breeding method." Suneson (1945) also introduced the use of genetic male sterility to facilitate crossing in composite cross populations of barley.

Jensen (1970) proposed a breeding strategy, the "diallel selective mating system," which he (Jensen, 1978) considered to be a form of "composite breeding." Both mass and recurrent selection procedures are employed in the DMS system and male sterility is used to facilitate crossing.

The rationale for using composite crosses was to allow natural selection to produce populations containing novel germplasm. Natural selection seldom acts in the direction favored by the breeder; the highest yielding and most disease resistant progenies are usually not perpetuated in a bulk population. A desire to produce an agronomically acceptable cultivar with novel germplasm, e.g., salt tolerance, and a realization that the expression of many characters can be strikingly modified by background genotype led to superimposing recurrent selection procedures on composite cross populations that were segregating for male sterility (cf. Ramage, 1987). R.F. Eslick suggested that the term "male sterile facilitated recurrent selection (MSFRS)" be used to describe these procedures (Ramage, 1975). Later, Eslick (1977) distinguished those composite crosses that had been made by hand-emasculatation from those that had used male sterility to facilitate crossing as "composite crosses" and "recurrent selection populations" (RSP's). He stated that population means could be shifted in RSP's by "rougeing undesirable types or by selecting only desired types." The two procedures differ in the generation in which selection is practiced and in the method used to recombine selections. With "rougeing," selection is done in the F₁ by removing undesirable plants and harvesting the rest in bulk. Recombination is effected by growing the F₂ in isolation and harvesting outcrossed seed set on male sterile plants to provide the F₁ for the next cycle. With "selection," desirable plants are selected from the F₂ and intercrossed by hand. The bulk F₁ is grown without selection to provide the F₂ for the next cycle. The merits of selecting F₁ vs. F₂ plants have been debated (Eslick & Ramage, pers. communic.).

The Montana/USAID Barley Project used recurrent selection by "rougeing undesirable types" to

develop populations containing broadbased resistance to several diseases (cf. Bockelman & Sharp, 1986), and a number of the RSP's have been registered as composite crosses. The USDA/ARS/University of Arizona barley program used "selecting only desirable types" to develop short-strawed, lodging resistant populations that were released as successive versions of CC XXXII (cf. Ramage, 1987).

As used by the USDA/ARS/University of Arizona barley program, the simplest form of MSFRS involves selecting large numbers of both male sterile and male fertile plants from a population segregating for both the desired character and male sterility, intercrossing the selections, bulking the crossed seed, and growing and harvesting the F₁. The F₂ provides the population for the next cycle of selection. New germplasm is introduced into the population in any cycle by crossing it onto male sterile plants. By growing the F₁ in an off-season nursery, a cycle of recurrent selection is made in one calendar year.

The basic program is suited for characters where selection based on an individual plant is effective. Effectiveness of selection will diminish in a closed recurrent selection program, as an equilibrium will be reached in which as many favorable gene combinations are broken up as are formed. Valid selection in a program may be extended by introducing new sources of germplasm into the population. Depending on the suitability of the introduced germplasm, it may be mass-backcrossed to the population a few times or carried as a separate program for a few cycles before introducing it into the population. This is equivalent to backcrossing to "pre-adapt" exotic germplasm to obtain parents for pedigree breeding programs.

For characters where selection based on an individual plant is not as effective as selection based on a progeny row, a system of isolating lines from the population and then backcrossing selected ones into the population is used. Male fertile spikes are selected (or more properly, collected) from the F₂ and their progenies grown in rows in the off-season nursery. A single plant is harvested from each F₃ row and the F₄'s are grown in "thick-thin" rows. These are two 3-meter rows, end-to-end, one planted with 200 seed and the other with 20 seed. Rows are selected based on the "thick" end, and a plant in the "thin" end is crossed onto a selected male sterile plant in the F₂ of the next cycle of recurrent selection. The purpose of the "thin" row is to provide pollen over an extended period which allows crosses to be made between early and late selections. Crossing selections back into the population not only permits more effective

selection, but the "more favorable gene combinations" are more likely to be preserved in the population.

MSFRS populations should continue to improve with each cycle and may be continued indefinitely and exploited regularly. The basic features that make MSFRS effective are: the generation and maintenance of a wide genetic base from which to select, the ability to make the large number of crosses necessary to obtain rare gene combinations, the opportunity to apply extreme selection pressure to large populations generated by the system, and the shortened time between cycles of effective selection.

Two approaches to using recurrent selection to develop disease resistant material have been used. One approach has been to develop disease resistant populations to provide parents for conventional breeding programs. The Montana/USAID Barley Project has used this approach to develop barley germplasm to be utilized by local breeders in less developed areas of the world (Eslick, 1977; Bockelman & Sharp, 1986).

The other approach has been to select for agronomic acceptability while trying to keep the genetic base of the population broad enough to include and retain disease resistance. Resistance is almost invariably found in unadapted material that cannot be used directly in breeding programs. The USDA/ARS/University of Arizona barley breeding program uses several tactics to accumulate genes for disease resistance in CC XXXII, an MSFRS population intended for high-yield conditions. Unadapted germplasm containing resistance genes is crossed onto CC XXXII and the resulting population is treated as a sub-population for several cycles of selection for agronomic type. The sub-populations are then crossed into CC XXXII. Lines are regularly extracted from CC XXXII, evaluated for disease reaction, and the resistant ones crossed back into CC XXXII. Another approach has been to grow CC XXXII in the presence of diseases and combine-harvest the material. The seed is screened for size and separated by density over a gravity table. The large, dense seed is presumed to have been produced by plants with an enhanced ability to reproduce in the presence of diseases. Plants are grown from the large, dense seed, and crossed back into CC XXXII.

In summary, breeding for yield in the presence of diseases (as opposed to breeding for disease resistance) by recurrent selection is the most effective means of obtaining locally-adapted, high-yielding, disease-tolerant cultivars. This presumption is based

on the following premises: that every character of every living organism is the product of an interaction between a specific genotype and a specific environment; that background genotype is a large component of any environment; that every character or combination of characters has a background genotype that is most favorable for the expression of that character or combination of characters; that for some characters, background genotype may be just as necessary for "most favorable expression" as the genotype of the character itself; and that recurrent selection is the most feasible means of simultaneous selection for a character and its background genotype.

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Molecular and Energetic Aspects of Induced Resistance in Barley

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Introduction

One of the most fascinating properties of plants is their capacity to protect themselves against pathogens occurring in their daily environment. This inherited potential for self-defense may, from both economical and ecological points of view, be considered as one of the most attractive means of plant protection and has been utilized for years by plant breeders for creating new varieties with resistance against important diseases.

Three basic types of disease resistance can be distinguished: partial resistance, race-specific resistance, and non-host resistance. Partial resistance depends on many host genes with additive effect. Alone, each of these genes is supposed to have a limited effect, but acting together they may provide a considerable, although not total, protection against pathogen attack (e.g., Jones *et al.*, 1982). Due to its polygenic nature, partial resistance has proved to be a stable feature, not vulnerable to changes in the composition of races in the pathogen population.

The second basic type of resistance is termed race-specific resistance. In contrast to partial resistance, it is usually governed by single (or few) genes with a high protective effect against some pathogenic races, but not against others. Race-specific resistance has been utilized for many years in breeding programmes for resistance against important diseases. One serious drawback related to race-specific resistance is, however, that resistant cultivars often lose their resistance after a few years. This is due to changes in the composition of the pathogen population resulting in the appearance of virulent races which can overcome the resistance genes used.

The effect of specific resistance genes in the host depends on the race which attempts to infect and, as demonstrated by Flor (1956), resistance results from interactions between the genetic systems of the host and the pathogen. The events leading to either resistance or susceptibility thus result from the

expression of genes in both the host and the pathogen.

The third type of natural defense systems against diseases in plants is termed non-host resistance. It is expressed by plant species not observed to be a host of a given pathogen species. Since all plants are resistant to most potential pathogens occurring in nature, non-host resistance reflects the limited host range of most pathogens.

An important aspect of the three types of disease resistance mentioned is that they depend on active defense reactions which are apparently induced (activated) in the host plant by pathogenic or potential pathogenic microorganisms, or even by saprophytes (Thordal-Christensen & Smedegaard-Petersen, 1988a; Gregersen & Smedegaard, 1989; Christiansen & Smedegaard, 1990). Hence, resistance is not a permanent condition of the host plant, but rather a potential capacity for defense which is expressed only when the host is attacked. Resistance thus seems to be conditioned by a subtle balanced gene regulation which ensures that defense reactions operate only during the time when they are needed.

Although resistance has been extensively studied from genetical, biochemical, and histological points of view, many fundamental questions concerning the way in which the plant pathogens interact with their hosts or non-hosts remain unanswered, and little is known of the molecular control of defense responses. It seems clear, however, that active resistance reactions are related to a multitude of physiological and biochemical changes which may play a decisive role in differentiating between resistance and susceptibility, and many of these resistance responses involve the activation of genes (Collinge & Slusarenko, 1987). Therefore, since active defense in

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plants seems closely related to an increased metabolic activity, the energetic consequences for the plant should be emphasized, and experimental evidences clearly suggest that induced resistance reactions may deplete the host of stored energy leading to reduction in plant growth and yield even in disease-free crops (Smedegaard-Petersen, 1989).

This paper discusses some of the newer results on induced resistance in barley against barley powdery mildew and the energy cost of the host associated with resistance reactions.

Induction of Resistance in Barley Against Powdery Mildew

Induced resistance following inoculation with the same or other microorganisms is well known from many host-pathogen interactions (Sequeira, 1983). It can be defined as active defense based on physical and chemical barriers elicited by preliminary inoculations with pathogens and non-host pathogens, or by the application of metabolic products from such organisms. It acts against subsequent infections by otherwise pathogenic organisms. In a broader sense, the term also includes resistance induced by abiotic stimuli. Two functionally different forms of induced resistance can be distinguished — systemic and localized (Kuč, 1982). Induced systemic resistance against a pathogen can be elicited by preliminary inoculation with a pathogen or a potential pathogen. This inoculation, termed inducer inoculation, conditions the host tissue to respond in a resistant fashion against a subsequent pathogen (termed the challenger) which is applied to plant parts distant to the site of induction. In contrast, induced local resistance is localized to the site of induction.

In interactions between barley and powdery mildew, *Erysiphe graminis* f.sp. *hordei*, Hwang and Heitefuss (1982) reported on induced systemic resistance, but most other studies have considered the induction of local resistance (Ouchi *et al.*, 1974, 1976; Stenzel *et al.*, 1983; Cho & Smedegaard-Petersen, 1986; Thordal-Christensen & Smedegaard-Petersen, 1988a). In all of these studies, the localized induced resistance appears to be much stronger than the systemic induced resistance reported by Hwang and Heitefuss (1982).

Cho and Smedegaard-Petersen (1986) and Thordal-Christensen and Smedegaard-Petersen (1988a) studied the resistance-inducing capacity of avirulent and virulent isolates of barley powdery mildew, *Erysiphe graminis* f.sp. *hordei*. Leaves of near-isogenic lines of the barley cultivar "Pallas" (Kolster *et al.*, 1986) were fixed in a horizontal position and

inducer-inoculated with avirulent or virulent races of barley powdery mildew (Figure 1). After the induction period, the inducer inoculum was removed and the leaves were challenge-inoculated with a virulent race of barley powdery mildew. Induction of resistance was assessed as percent reduction in number of mildew colonies produced by the virulent challenger race in relation to the number of colonies developed on a non-induced control.

The results from these experiments showed that both avirulent and virulent mildew races are rapid and strong inducers of resistance. For both races, an induction period of ½ h induced significant resistance, and an induction time of 6 h induced 70-75% protection against a compatible challenger race (Cho & Smedegaard-Petersen, 1986). At high densities of inducer inoculum, the degree of resistance obtained exceeded 90% (Thordal-Christensen & Smedegaard-Petersen, 1988a). The longevity of resistance was not determined, but persisted for at least 72 h.

A series of experiments was conducted in which the induction period was extended to 24 h. This series also included wheat powdery mildew, a non-host pathogen on barley, as an inducer (Figure 2). All of the three inducers (avirulent and virulent races of barley powdery mildew and an isolate of wheat powdery mildew) yielded about the same degree of protection after induction periods of up to 10 h. At induction periods longer than 10 h and low concentrations of inducer inoculum (6.5 and 20 conidia/mm²), there was a marked increase in the resistance-inducing capacity of the avirulent race related to the virulent.

Recent studies (Gregersen & Smedegaard, 1989; Christiansen & Smedegaard, 1990) have shown that not only pathogens and non-host pathogens, but also pure saprophytes, are capable of inducing resistance. When barley plants were inoculated with the saprophytic fungus *Cladosporium macrocarpum*, up to 37% protection against subsequent infection by barley powdery mildew was found. That saprophytic fungi possess the capacity of inducing resistance is supported by Sahashi *et al.* (1989) who found that barley plants grown under germ-free conditions showed increased susceptibility to barley powdery mildew.

Induced Resistance Is Unspecific and Involves Different Types of Resistance

Induced resistance in barley against barley powdery mildew appears to be unspecific since it seems to be unrelated to race specificity and can occur in barley lines with or without known resistance genes

(Cho & Smedegaard-Petersen, 1986; Thordal-Christensen & Smedegaard-Petersen, 1988a; Gregersen & Smedegaard, 1989). These findings are in agreement with those of Schönbeck *et al.* (1980) who used different combinations of inducers, plant species, and pathogens; they concluded that one inducer elicited resistance to various fungi, that the response was found in all plant species tested, and that the same response was elicited by various inducers. They further concluded that the induced resistance was effective only against obligate parasites.

Two types of induced defense seem to be involved in the barley-powdery mildew interaction (Cho & Smedegaard-Petersen, 1986). If the inducer race, either avirulent or virulent, is removed before appressorial formation, the resistance appears as a reduction in the number of mildew colonies developed by the challenger race but without any change in the infection type and sporulation capacity. However, if the avirulent inducer race remains on the leaf along with a virulent challenge race inoculated onto the leaf 1 h after inducer inoculation, there is a change in infection type produced by the challenge race from type 4 to type 1-3 (reduced sporulation capacity) and the development of numerous hypersensitive necrosis.

Altogether, there seem to exist at least two levels of induced resistance in the barley-powdery mildew interactions. Avirulent and virulent races as well as wheat powdery mildew induce rapid and early unspecific resistance appearing as a reduction in the number of mildew colonies produced by challenge inoculation. As seen in the next paragraph, this early step may be initiated by penetration attempts from the primary germ tube. At induction periods longer than 8-10 h, avirulent races seem to induce an additional resistance step which increases the final level of resistance. This latter step is probably initiated by appressorial penetration attempts.

Cytological and Molecular Cell Responses Associated with Induced Resistance

Induced resistance is the visible end-result of a series of biochemical and molecular events including many unelucidated steps. Important questions in exploiting induction of defense in interactions between plants and their pathogens concern the initial signals leading to gene expression in host cells and the mechanisms of signal transduction between the pathogen and host. The term "elicitor" has been used to designate substances which activate defense

reactions in plants (e.g., Darvill & Albersheim, 1984; Dixon, 1986). Even though elicitors have been extensively studied in recent years, their role in defense processes *in vivo* is still unclear and no clear evidence has appeared concerning the initial triggering processes leading to induction of gene expression (Lamb *et al.*, 1989). An important aspect is that most elicitors reported are unrelated to race specificity, although certain products of avirulence genes show specific elicitation activity (Keen *et al.*, 1990).

In the interactions between barley and barley powdery mildew, no elicitors have been described so far. However, the finding that the primary germ tube of germinating conidia interacts with the host epidermal cells within 2-4 hours after inoculation (Kunoh *et al.*, 1978) coinciding with the activation of resistance (Thordal-Christensen & Smedegaard-Petersen, 1988a) suggests that the primary germ tube may play a role in the induction process. The primary germ tube is a short non-appressorial tube which makes unsuccessful attempts to breach the cell wall leading to the formation of cell wall appositions, papillae, appearing beneath the site of attempted penetration within 4 hours after inoculation (Kunoh *et al.*, 1978; Kunoh, 1982). The penetration attempts by the primary germ tube and the cytological events associated with it precede appressorial penetration and the subsequent formation of haustoria by 3-4 hours (Kunoh *et al.*, 1978), and appears to be the first visible interaction between the host tissue and the pathogen. That the primary germ tube may act as an inducer of resistance also appears from the work by Woolacott and Archer (1984), who found that the infection process by an appressorium was inhibited in cells which had previously been affected by penetration attempts of primary germ tubes. At the cytological level, it has been shown that induced resistance in barley against barley powdery mildew leads to an increased formation of fluorescent papillae at the attempted penetration sites of the challenger pathogen (Ebrahim-Nesbat & Schönbeck, 1985; Shashiyama, 1986).

Although papillae occur in both compatible and incompatible interactions, they have been assigned a role in resistance because penetrating infection hyphae are often stopped at the papillae stage (Kita *et al.*, 1980; Koga *et al.*, 1988). The efficiency of papillae as barriers against infection seems to be related to their size, fluorescence, and rapidity by which they are formed (Kita *et al.*, 1980; Skou *et al.*, 1984; Smart *et al.*, 1986). Thus, Thordal-Christensen & Smedegaard-Petersen (1988b) found that the size of fluorescent papillae beneath unsuccessful challenger

infection units increased when resistance was induced in the leaf. The latter suggests that induction of resistance involves the activation or sensitization of host tissues which, upon subsequent penetration attempts, react with enlarged fluorescent papillae which, in turn, inhibit or stop the fungus.

The cytological evidence indicates that papillae contain polyphenolic material ("lignin-like" material), callose, and protein. All these components, along with PR-proteins and phytoalexins, are believed to have a role in inhibiting pathogen development (e.g., Aist & Israel, 1986; Boller, 1987; Collinge & Slusarenko, 1987). Furthermore, there is evidence that increases of enzyme activities associated with the production of polyphenols correlates with papillae formation in infected tissues (Kerby & Somerville, 1989; Shirashi *et al.*, 1989), but 1,3- β -D-glucan synthetase activity levels do not increase with callose production (Pedersen, 1990).

Little is known at the molecular level about the responses underlying defense reactions in barley against barley powdery mildew. Specific genes for resistance are known empirically, and have been used widely in breeding for new resistant varieties. Their function is, however, unknown, and so far no such genes have been cloned. In contrast to specific resistance genes, a number of resistance response genes against powdery mildew have been cloned. Davidson *et al.* (1987) thus found an increase in specific mRNA species in barley 12-35 hours after inoculation with barley powdery mildew, indicating gene expression at the time of penetration attempts from appressorial germ tubes. By the application of 2D-PAGE, Gregersen *et al.* (1990) found that inoculation of barley with wheat powdery mildew, which is a non-host pathogen of barley, resulted in the expression of a specific set of genes. Two-dimensional polyacrylamide gel electrophoresis of *in vitro* translation products, made from RNA isolated from inoculated and uninoculated barley leaves, showed the appearance of about 10 new polypeptides 2-4 hours after inoculation. The early induction of gene expression found by Gregersen *et al.* (1990) correlates with the time of interaction between the primary germ tube of the conidia and the epidermal cells of the host, and it may reflect resistance responses induced at the papillae stage as compared to the results by Davidson *et al.* (1987) who used a barley-powdery interaction with resistance based on hypersensitivity.

The experiments by Gregersen *et al.* (1990) suggest that the resistance response of barley to infection attempts by wheat powdery mildew is related to early gene expression and a subsequent rapid

accumulation of new mRNA's 2-4 hours after inoculation. The results also suggest that the primary germ tube of germinating conidia may be involved in the induction of gene expression.

A cDNA library was prepared using RNA extracted from barley leaves 6 hours following inoculation with wheat powdery mildew and screened for sequences induced by mildew using a probe enriched by subtractive hybridization. Six cDNA clones, representing four different genes were isolated and their expression studied in relation to inoculation with wheat mildew, and compatible and incompatible barley mildew isolates (Thordal-Christensen *et al.*, in prep.). The expression of all four genes increases 4-6 hours after inoculation in all interactions (Figure 3), and high levels of each mRNA are maintained until 15-24 hours after inoculation. Expression of these four genes corresponds with the results obtained by analysis of *in vitro* translation products (Gregersen *et al.*, 1990; Thordal-Christensen *et al.*, in prep.), supporting a role for them in papilla resistance. Cross-hybridization and sequence analysis demonstrated that none of these cDNA's represent the genes cloned previously by Davidson *et al.* (1987), or to the thaumatin-like PR protein of barley (Bryngelsson & Gr  n, 1989), or to leaf thionins (Bohlmann *et al.*, 1988).

DNA sequence analysis of the gene exhibiting the most marked relative induction demonstrates that this cDNA clone represents a peroxidase gene related to those of turnip (Mazza & Welinder, 1980), potato (Roberts *et al.*, 1988), tobacco (Lagrimini *et al.*, 1987), and horseradish (Fujiyami *et al.*, 1987). This clone hybridized more strongly to a cloned wheat peroxidase gene induced by barley powdery mildew (Schweizer *et al.*, 1989) than to other barley peroxidase clones (Rasmussen *et al.*, and pers. commun.; Brandt *et al.*, 1990). Peroxidase enzyme activity increased between 8 and 16 hours after inoculation in both compatible and incompatible interactions (Kerby & Somerville, 1989), thus corresponding to changes in levels of the cloned mRNA. Peroxidases are thought to have a role in lignin and suberin production as well as cross-linking of cell wall proteins (Lewis & Yamamoto, 1990; Varner & Lin, 1989).

A second clone represents sucrose synthetase and its sequence is very similar to both cereal (Bhave *et al.*, 1990) and potato (Salanoubat & Belliard, 1987) sequences. This gene is not as strongly induced by mildew as is peroxidase. It is not clear whether its induction implies a role for the enzyme in providing energy for resistance, or whether it is involved in, for example, callose production by

providing UDP-glucose as a substrate for callose synthetase in the papillae.

The sequence of three of the clones shows striking homology to a gene family known from animals and yeast encoding a 94 kD stress-induced polypeptide known variously as endoplasmin or glucose-regulated protein (grp - Kulomaa *et al.*, 1987; Mazzarella & Green, 1987), proteins induced by stress which are nevertheless constitutively expressed to a high level (Hardesty & Kramer, 1989). Grp proteins are closely related to the 90 kD heat shock protein family. These proteins are located in the endoplasmic reticulum (Mazzarella & Green, 1987) and it is thought they act as chaparons, controlling the assembly of proteins from their constituent subunits (Ellis, 1987; Hardesty & Kramer, 1989). We speculate that they have a role in helping proteins destined for export to developing papillae.

There is no evidence to link any of these genes to race-specific resistance, but papillae and induced resistance are recorded in both compatible and incompatible interactions. The coincidence of both these phenomena with the expression of our cDNA clones does imply a role for the products in resistance. We are currently using *in situ* hybridization to determine whether their expression is systemic in the leaf or localized to epidermal cells in contact with the penetrating spores, and whether there are differences between compatible and incompatible interactions at the cellular level. We are also attempting to measure the corresponding enzymes with the help of cytohistological techniques and to determine the location of the proteins with the help of antibodies. We are conducting sequence analysis of the remaining clones, and screening cDNA libraries obtained using barley mildew as the inducer organism for further genes, since we know from our *in vitro* translation studies that at least 10 genes are up-regulated as part of the resistance response, in order to obtain a more complete picture of the resistance response in relation to induced resistance.

Energetic Consequences of Active Resistance on Plant Growth and Yield

Obviously resistance reactions are associated with enhanced biological activities including the accumulation of host-synthesized antimicrobial substances, syntheses and deposition of lignin-like materials, enhanced syntheses of post-infectious polypeptides, increases in certain hydrolytic enzymes such as chitinase and glucanase, accumulation of hydroxyproline

rich glycoproteins and increased quantities of new mRNA species (Sequeira, 1983; Manners *et al.*, 1985; Collinge & Slusarenko, 1987; Davidson *et al.*, 1987; Nicholson *et al.*, 1988; Sahashi *et al.*, 1989; Gregersen *et al.*, 1990).

That such resistance-related increases in biosynthetic activity require considerable amounts of energy was demonstrated by comparing the respiration of incompatible and compatible interactions between barley and the barley powdery mildew fungus (Smedegaard-Petersen & Stølen, 1981; Smedegaard-Petersen, 1982). After a single inoculation, resistant leaves reacted with a rapid temporary respiratory increase, already detectable 8 hours after inoculation, returning to the level of the non-inoculated control after 3 days. When plants were subjected to three successive inoculations spaced with intervals of two days, the oxygen uptake initially followed the same pattern, but instead of returning to the normal level, the rate stabilized at a level significantly higher than that of the non-inoculated controls. Thus, repeated inoculation of barley with an avirulent race of the powdery mildew fungus causes a permanent increase in the rate of respiration. The pronounced increase in oxygen uptake coincided in time with the appearance of papillae beneath the appressoria (Kunoh *et al.*, 1978), and the synthesis and accumulation of resistance related mRNA species and proteins (Manners *et al.*, 1985; Davidson *et al.*, 1987; Gregersen *et al.*, 1990).

In order to investigate whether the increased energy demand in inoculated, resistant plants is sufficient to reduce plant yield, experiments were carried out in growth chambers (Smedegaard-Petersen & Stølen, 1981). Although resistant plants did not show any visible disease symptoms after continuous inoculation with an avirulent race, the grain yield was significantly reduced by 7% and the kernel weight by 4%. The yield of grain protein was reduced by 11% and straw length by 5%.

The fact that highly resistant barley plants did not show any visible symptoms after inoculation with the pathogen does not, however, mean that the plants are not affected. The results suggest that mildew resistant barley plants respond to inoculation by energy-demanding defense reactions that drain the stored host-energy otherwise available for buildup of yield components.

In the light of these results, it is of interest that we have recently identified a gene for sucrose synthetase among four cDNA clones representing genes induced by powdery mildew (Thordal-Christensen *et*

al., in prep.). The increased gene sucrose synthetase activity may imply a role for this enzyme in the energy balance of leaves undergoing a resistance response. However, it is also possible that sucrose synthetase has a direct role in callose biosynthesis by providing UDP-glucose from sucrose transported into cells which are developing papillae in response to pathogen penetration.

Extensive studies (Tolstrup, 1984; Smedegaard-Petersen & Tolstrup, 1985, reviewed by Smedegaard-Petersen, 1989) have demonstrated that commonly occurring leaf saprophytes have the capacity for reducing crop yield by inducing energy-requiring defense reactions in much the same way as do incompatible races of powdery mildew. Leaf saprophytes are present in large amounts on the aerial parts of field crops where they colonize the lower dead leaves and deposit large quantities of spores on the upper green leaves. In general, these saprophytic leaf fungi are unable to infect vigorously growing green leaves, but the studies referred to above clearly suggest that saprophytic filamentous leaf fungi, especially species of *Cladosporium*, elicit active, energy-consuming defense reactions similar to those elicited by spores of avirulent barley powdery mildew. This was demonstrated in extensive field trials with barley where chemical control of leaf saprophytes with fungicides increased the grain yield by 16% even though there was no or little disease present in the untreated control plots. The results were confirmed in yield experiments in controlled growth chambers, where barley plants were inoculated six times during the growing season with the leaf saprophyte *Cladosporium macrocarpum*, which is one of the most common saprophytes in Danish barley fields (Tolstrup, 1984; Smedegaard-Petersen & Tolstrup, 1985). Although the inoculated plants had no visible disease symptoms, the grain yield was reduced by 9%, the kernel weight by 2%, the number of kernels per spike by 7%, and the straw length by 1.6 cm. In addition, the chlorophyll content of inoculated plants was reduced, most markedly in the flag leaves. The yield-reducing effect of saprophytes is most marked in dense crops with a humid microclimate that promotes fungal growth and propagation.

Practical Application of Induced Resistance

One of the few successful attempts to make use of induced resistance for practical disease control has been made by Schönbeck and co-workers. By spraying barley and wheat crops with culture filtrates from

the bacterium *Bacillus subtilis*, they recorded a significant reduction of attacks by powdery mildew and a significant increase in grain yield (Schönbeck *et al.*, 1980). The pathogen produced smaller mildew colonies on sprayed plants, and the sporulation rate and formation of cleistothecia were reduced. Remarkable yield increases exceeding 30% were recorded in filtrate-treated crops. This was a higher increase than obtained by controlling the powdery mildew with fungicides (Dehne *et al.*, 1984; Oerke *et al.*, 1989).

The astonishing effect of bacterial culture filtrate on grain yield, however, was not exclusively a result of induced resistance, but rather a more complex effect on host physiology including a marked delay of senescence. This conclusion was strengthened by the finding that reduction of disease severity and increase in grain yield were not strongly correlated.

Although the results obtained by culture filtrates of *Bacillus subtilis* on grain yield cannot be fully ascribed to induced resistance, the results are encouraging and give inspiration to further research on the applicability of induced resistance in practical disease control.

Summary

Both virulent and avirulent races of barley powdery mildew as well as races of wheat powdery mildew, a non-host pathogen on barley, induce resistance in barley against a virulent race of barley powdery mildew within one-half hour of induction. There seem to be two levels of induction involved in the interactions between barley and powdery mildew. The first step, which is non-specific as it is induced by both virulent, avirulent, and pathogenic races of powdery mildews, acts by reducing the number of mildew colonies produced by the challenger race. The second step is induced at the time of appressorial penetration by avirulent races of *Erysiphe graminis* f.sp. *hordei* only, and it results in further increase of resistance. The energetic consequences of active defense in barley against powdery mildew are reflected in an increased respiratory rate and a reduction in grain yield by up to 7%.

The early induction of resistance correlates with cytological and biochemical changes in the host cells at the site of interactions between the inducer and host, as well as with the activation of a number of putative resistance response genes. This was strongly suggested by the appearance of about 10 new mRNA species which could be detected by their *in vitro* translation products from 2-3 hours after inoculation. Screening of a cDNA library prepared using

RNA isolated from barley leaves 6 hours after inoculation with wheat powdery mildew by subtractive hybridization, yielded cDNA clones representing four different DNA species. Northern blot analyses utilizing each clone demonstrated increased mRNA levels 4 hours after inoculation, thus confirming that the cDNA clones represent resistance response genes. DNA sequence analysis shows that three of the clones represent a peroxidase, a sucrose synthase, and an endoplasmic reticulum chaperone (a heat shock-like gene).

An important aspect of induced active resistance, which was previously demonstrated in our laboratory, is that it depends on a greatly increased biosynthetic activity which occurs at the expense of stored host energy. Thus, not only avirulent races of barley powdery mildew, but also common leaf saprophytes, elicit energy-requiring defense reactions which may significantly reduce plant growth and grain yield even though no visible symptoms are observed.

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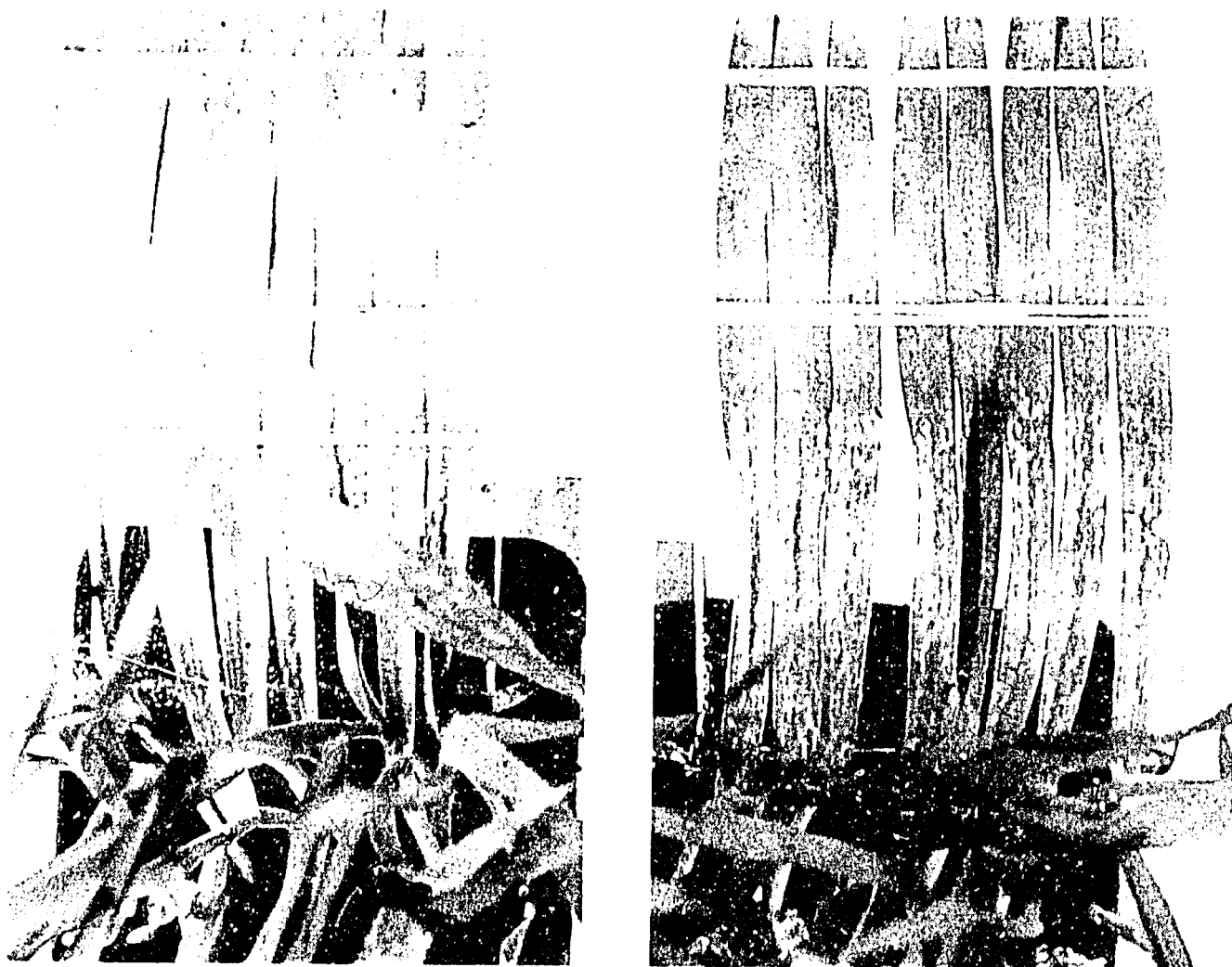


FIGURE 1. Induced resistance in near-isogenic line of the barley cultivar Pallas with the resistance gene *MI-a*. The avirulent inducer race C15 of *Erysiphe graminis* f.sp. *hordei* was applied to the leaf area between the 2 strings of the 8 leaves to the right. After an induction time of 6 hours, the inoculum was removed and all leaves were challenge-inoculated with the virulent race A6.

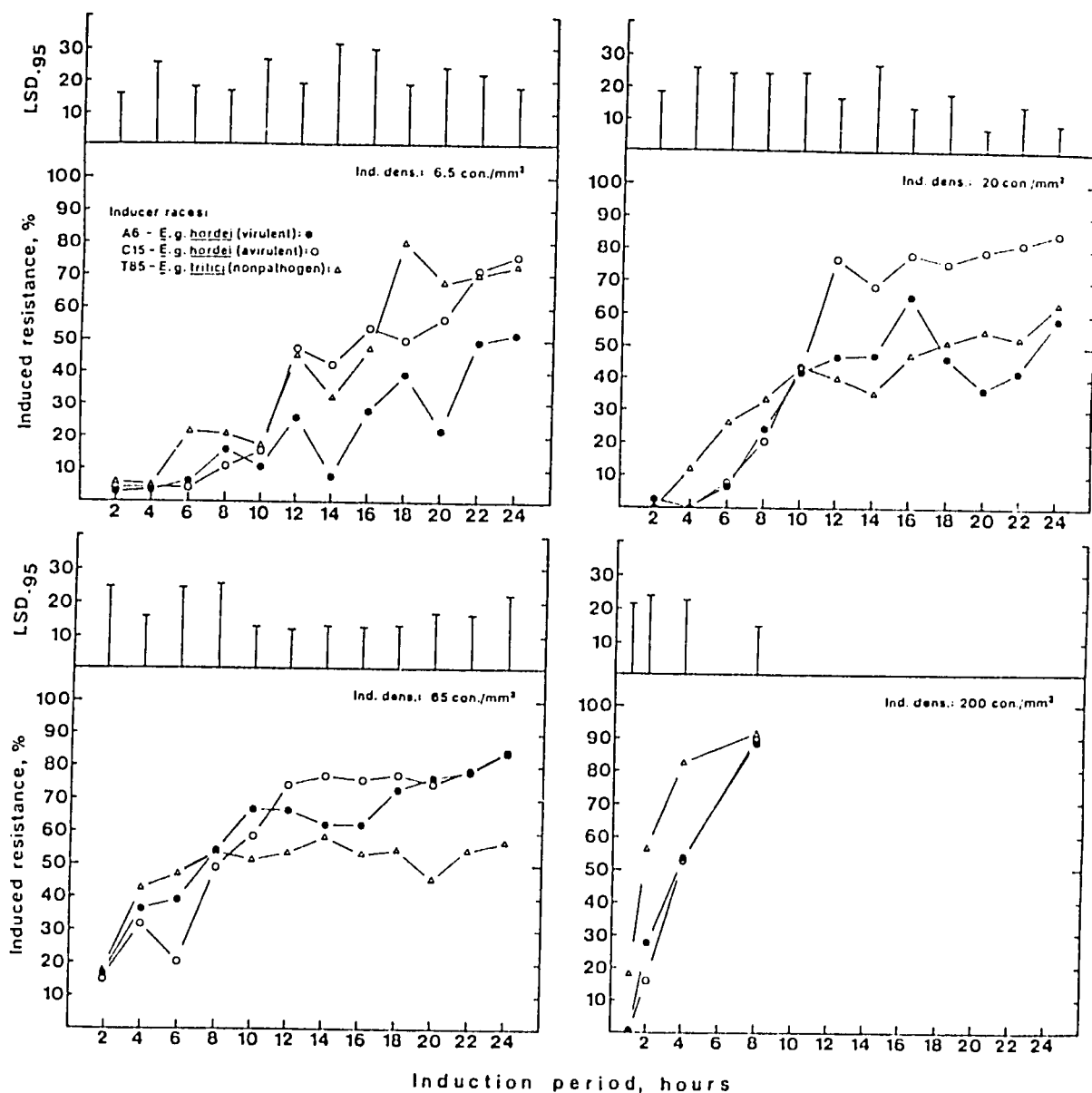


FIGURE 2. Comparison of the resistance induced in a near-isogenic line of the barley cultivar Pallas with the resistance gene *Ml-a*. Resistance was induced by the virulent race A6, and the avirulent race C15 of *Erysiphe graminis* f.sp. *hordei*, and by the non-pathogenic race T85 of *E. graminis* f.sp. *tritici*. The comparison was made at 4 different inoculum densities and in 13 different induction periods. Mean values of 3 replications. (Data from Thordal-Christensen and Smedegaard-Peterson, 1988.)

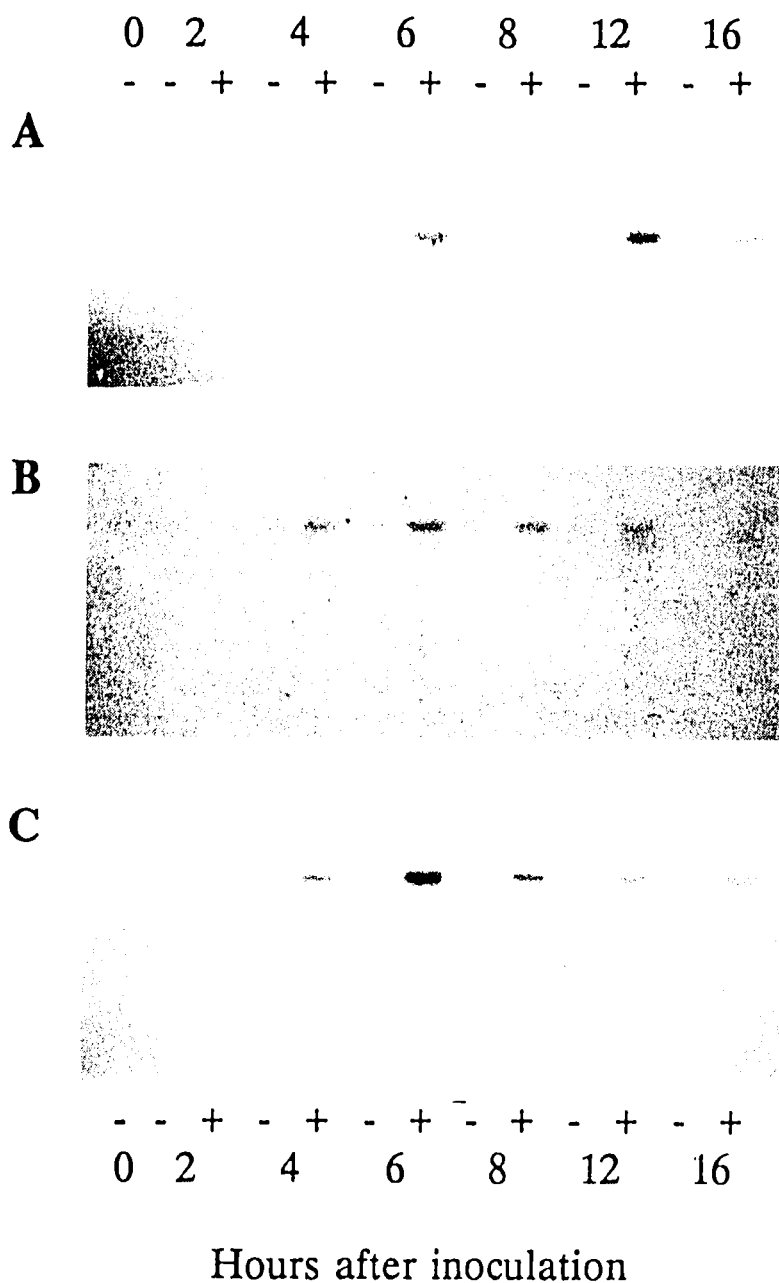


FIGURE 3. Northern blots of total RNA from barley leaves extracted at different time points after inoculation with an avirulent race of *Erysiphe graminis* f.sp. *hordei* (+) studied versus an uninoculated control (-). The blots were hybridized with three putative barley resistance response cDNA clones isolated in our laboratory: (1) the peroxidase cDNA, (2) the sucrose synthase cDNA, and (3) the endoplasmic reticulum cDNA. The differences in band intensities between the cDNA clones do not reflect the amounts of the specific transcripts.

Recombinant Inbred and Doubled Haploid Lines: The Biology, Technology, and Utility

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I have taken the liberty of adding two key terms to the title of this presentation: "doubled haploids" and "utility." Doubled haploid (DH) technology has the potential to tremendously increase the rate of genetic improvement of barley in arid and semi-arid environments. The biology and technology of generating DH lines has been the subject of extensive review, and I make no pretense of providing the latest data on protocol efficiency. Rather, I will quickly review the technology of DH line production, using data from North American labs active in this area, and then proceed to a discussion of current and potential applications of these materials. As I will show, current technology allows for routine DH lines production in barley. We now face the challenge of exploiting the capabilities this technology offers.

A distinction should be made at the outset between the terms "recombinant inbred" (RI) and "doubled haploid" (DH). The former has been used in the literature to describe inbred lines randomly derived through repeated cycles of selfing one individual per line per generation for five or more generations beyond the F₂ (Knapp *et al.*, 1990). An example of this approach is single seed descent (SSD). The latter term describes inbred lines derived from male or female gametic cells and/or tissues. The key difference between a set of SSD lines and a set of DH lines derived from the same F₁ lies in the number of recombination events. The number of meioses has important implications for genetic analysis and breeding (Cowen, 1988). Throughout this presentation, the distinction between RI and DH lines will be preserved, and unless otherwise specified, DH lines will be assumed to have been derived from the F₁ generation of a cross between two inbred lines.

The attraction of RI and DH lines, regardless of their method of derivation, lies in the fact that they provide a resolution to the fundamental dilemma facing researchers interested in the genetics of self-pollinated species: Genetic analyses and breeding procedures require the intermating of inbred lines, yet much of the gene action expressed in the generations immediately following the cross is transient and

cannot be exploited. Historically, this has led to some rather unsatisfactory results.

Mendelian analyses traditionally have been based on F₂ and testcross progeny, but these genetic stocks are transitory and cannot be duplicated. Misclassification is more likely to occur in F₂ progeny due to partial dominance that hampers classification of heterozygotes. Completely homozygous DH lines allow for replicated evaluations, if necessary, and eliminate any bias that may be attributed to heterozygosity.

Quantitative genetic studies in self-pollinated species, such as estimation of combining ability effects and genetic parameters, have often been based on individual early generation plants or, at best, families. For example, estimating the heritability of grain yield, based on the performance of individual F₂ plants derived through a diallel mating, is of dubious utility. Reasonable measures of trait performance can be obtained only by extensive, multi-location, replicated evaluation of homozygous genotypes.

Accelerated, random advance of RI lines derived from an F₁ was early recognized as a solution to the problems plaguing estimation of quantitative genetic parameters in self-pollinated species. Single seed descent (SSD), sometimes coupled with off-season generation advance, remains a powerful tool in breeding and genetic analyses.

Nonetheless, a more elegant and potentially more efficient approach to production of inbred lines was to be found in exploiting the alternation of generations. By regenerating plants from cells and/or tissues of the gametophytic generation of a heterozygous donor and subsequently capitalizing upon induced or spontaneous chromosome doubling, arrays of inbred individuals could be developed in a relatively short time. A milestone in barley genetics was the discovery that crosses of *Hordeum vulgare* with *Hordeum bulbosum* led to the production of

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haploid embryos, due to the elimination of *H. bulbosum* chromosomes (Kasha & Kao, 1970). Since no endosperm is formed, the haploid embryo must be rescued and cultured on nutrient media for plant regeneration.

Of the haploid techniques currently available in barley, the *Hordeum bulbosum* method, as it bypasses the callus phase putatively responsible for somaclonal variation, is arguably the most appropriate for capitalizing upon sexual, as opposed to culture-induced, variation (Huang *et al.*, 1984). The *bulbosum* method has been used in numerous programs, but genotype specificity, or "incompatible responses," restricted its use to certain genotypes (Pickering & Hayes, 1976; Bjornstad, 1986). In winter habit barley, where the vernalization requirement complicates SSD and off-season advance, certain genotypes have shown low levels of *H. bulbosum*-mediated haploid production (Devaux, 1987).

Haploid production efficiency (HPE) with the *bulbosum* method is influenced by a number of factors and their complex interactions, including genotypic effects of *H. vulgare* (Pickering, 1983), the interaction of *H. vulgare* and *H. bulbosum* (Simpson *et al.*, 1980), and culture environment (Jensen, 1977). In general, HPE can be expressed as: $HPE = (\text{seeds/florets})/(\text{embryos/seeds})(\text{plants/embryos})$.

We have developed an *in vitro* floret culture technique that considerably increases the efficiency of *H. bulbosum*-mediated haploid production and allows for DH production from diverse germplasm arrays (Chen & Hayes, 1989; Hayes & Chen, 1989). In a comparison of *in vitro* floret vs. tiller culture, we found that the highest haploid production efficiencies were achieved with floret culture, a technique in which barley florets pollinated with *H. bulbosum* are cultured on modified N_6 media containing 0.5 mg L^{-1} kinetin and 1.2 mg L^{-1} 2,4-D. Floret culture efficiencies ranged from 20 to 48%, while detached tiller culture efficiencies ranged from 6 to 31%.

In vitro floret culture allows for efficiencies of *H. bulbosum*-mediated DH production suitable for both breeding and genetic analyses. Some of these applications will be detailed later. Before proceeding to androgenetic DH systems, a brief discussion of the merits of gynogenetic vs. androgenetic DH production is in order.

Successful use of DH lines in a breeding program requires that they are comparable to conventionally derived lines in agronomic performance and stability. Gamete selection, if present, must be unrelated to, or in favor of, agricultural fitness. For linkage

analyses, however, DHs must represent a random sample of F₂ gametes and no portion of the genome should be preferentially transmitted to the progeny.

Schon *et al.* (1990) tested the hypothesis that *Hordeum bulbosum*-derived DH lines are a random sample of F₂ gametes. We assayed a total of 23 morphological, protein, and RFLP markers. DH and F₂ progenies derived from a cross between a multiple marker stock and cultivar "Apex" were used to test segregation of alleles at marker loci dispersed throughout the barley genome. Goodness-of-fit tests at 23 loci revealed that 42 *Hordeum bulbosum*-derived DH lines from the cross MMS x Apex represent a random sample of F₂ gametes. That is, no selection for these loci, or for loci closely linked to them, occurred during the doubled haploid production process. Distorted segregation, however, was present in an F₂ population from the same cross.

Powell *et al.* (1986a,b) compared *Hordeum bulbosum* and anther culture-derived lines using both Mendelian and quantitatively inherited traits. They reported aberrant segregation for three out of five major genes for the microspore derived lines, and in one case, segregation of *Hordeum bulbosum*-derived DHs did not fit the hypothesized ratio (Powell *et al.*, 1986a). Based on a comparison of seven quantitative traits evaluated in field tests, Powell *et al.* (1986b) concluded that gamete sampling is random only for the *Hordeum bulbosum* technique and is, therefore, the preferred method for production of DH lines to be used in genetic analyses and breeding.

Gametophytic selection and/or somaclonal variation attributable to extended callus phases are limitations to androgenetic DH production imposed by current technology. However, considerable strides have been made in both anther and microspore culture, techniques whose potential efficiency far surpasses that of *H. bulbosum*-mediated haploid production. Factors in common to both anther and microspore culture that dictate ultimate efficiency are: (1) parent plant vigor, (2) spike pretreatments, (3) culture conditions, (4) media conditions, and (5) genotype. This final consideration is of particular importance.

A notable milestone in barley anther culture was the increased efficiency achieved with alternative carbohydrate sources. Unfortunately, the patenting of maltose as a carbohydrate source for barley anther culture (U.S. patent no. 4840906) has limited publication of protocols and efficiency data where this compound has been used without authorization of the patent assignee.

Preliminary data of Hou and Ullrich (1990) are presented for the sake of comparing the relative efficiencies of anther culture vs. *H. bulbosum*-mediated haploid production. Using a cold pretreatment of 35 days, between 5 and 45 green plants per 100 anthers were obtained using three spring barley genotypes. However, as only 3 to 20% of the embryooids produced actually produced green plants, considerably greater efficiencies should be realized with modifications of regeneration media and protocols.

Microspore culture offers even greater potential efficiencies than anther culture and has the following advantages: (1) it permits observation of microspore development; (2) it allows for the identification and sorting of specific microspores; (3) it avoids physical and chemical hindrances associated with the anther; (4) it simplifies mutagenesis and transformation; and (5) it allows for selection of single microspores, or calli derived from them. Preliminary data from microspore culture work at the University of Guelph using the winter 2-row cultivar "Igri" are impressive: 266 green plants/100 anthers (Kasha *et al.*, 1990).

Continued improvements in DH technology, built on a fundamental understanding of cell and tissue biology, will likely lead to repeatable, high efficiencies of DH production in diverse germplasm arrays. Depending on resources and objectives, chromosome elimination, anther culture, and microspore culture will all have a role to play in breeding and genetic analyses. The point of the foregoing discussion is that DH production is efficient and practical, and can be incorporated into any barley improvement program. The issue is clearly not how to produce DH lines, but how to use them.

I will frame my discussion of the utility of DH lines for germplasm enhancement and genetic analysis in the context of my research group's current activities. Much of our effort is directed at enhancing winter barley germplasm resources; recurrent selection, a technique designed to increase the frequency of favorable alleles in individuals in a population, is the breeding method of choice for such an endeavor. Advantages of recurrent selection are: (1) there is a low probability of random fixation of alleles controlling traits of low heritability; and (2) linkage blocks may be broken, resulting in increased genetic variability. Dr. Ramage has eloquently reviewed the use of recurrent selection for disease resistance breeding in barley; I will only point out how DH technology can facilitate recurrent selection strategies.

The effectiveness of recurrent selection in cross-pollinated crops is demonstrated (Hallauer & Miranda,

1981). There is good evidence that recurrent selection with intermating can be more effective than selfing and subsequent selection in self-pollinated crops (Ramage, 1977; Payne *et al.*, 1986; Reinhold, 1990). These studies have shown the superiority of recurrent selection strategies over conventional selfing methods for a range of quality, agronomic type, and disease resistance traits.

Several authors have suggested the possibility of using doubled haploids in recurrent selection programs. Kasha and Reinbergs (1981) pointed out the applications of haploidy in sampling male sterile-facilitated recurrent selection populations. Choo *et al.* (1979) presented a cyclic selection program in which a number of parental cultivars are crossed in a partial diallel, and doubled haploids obtained from the resulting F1's. Hayes and Stucker (1989) recently presented statistical considerations in implementing doubled haploid recurrent selection based on a circulant partial diallel mating.

The application of recurrent selection strategies to self-pollinated cereals, particularly those of winter habit, has been limited by cycle time. After cycles of intermating, effective selection for quantitatively inherited traits requires near-homozygosity in lines to be selected for the next cycle of intermating. Conventional accelerated approaches to homozygosity, such as single seed descent (SSD) and off-season nurseries, require relatively long cycle times and are not practical in winter barley. The use of doubled haploids — derived via microspore culture, anther culture, or the *Hordeum bulbosum* technique — reduces cycle time and offers advantages for both applied breeding and molecular marker analysis.

In addition to MSFRS, which will be addressed subsequently in the context of a proposed modification employing DH production, we are currently involved in doubled haploid recurrent selection (DHRS) based on a systematic mating. The theory and practice of DHRS in spring barley, based on a complete diallel mating, are described by Choo *et al.* (1979) and Patel *et al.* (1985). Stuthman and Stucker (1975) described the application of recurrent selection to an oat population generated via a complete diallel mating and advanced via single seed descent. On theoretical grounds, Gallais (1988) recently proposed "single doubled haploid recurrent selection" as the preferred method for simultaneously improving population performance and producing inbreds for evaluation as potential varieties.

Hayes and Stucker (1989) presented the use of a circulant partial diallel (CPD) mating design

(Kempthorne & Curnow, 1961) for DHRS, offering a straightforward approach to using doubled haploids to: (1) improve a population of inbred lines, (2) develop inbreds for evaluation as potential varieties, and (3) estimate pertinent genetic parameters. Our contribution was unique only with respect to providing a unified presentation of rationale, expectations, and implementation of recurrent selection in a population of barley doubled haploids derived via a circulant partial diallel mating.

As any given set of adapted parents cannot be construed as a random sample of winter barley germplasm, a fixed effects model is most appropriate (Baker, 1978). However, should one wish to use this procedure for estimation of genetic variances, the population of doubled haploids, representing a random sample of F₂ gametes (Schon *et al.*, 1990), may be identified as a base population in which to define a set of genetic parameters (Hanson & Weber, 1961).

A CPD mating design allows sampling of a large germplasm array with a reduced number of crosses via a balanced design in which each parent is involved in the same number of crosses. Crosses are allocated as described by Kempthorne and Curnow (1961). If, for example, each of 15 parents are mated with 8 others and reciprocals are excluded, a total of 60 cross combinations are produced. If 20 doubled haploids are used to sample each cross, as suggested by Choo *et al.* (1982), 1200 doubled haploid lines are generated.

Breeding objectives will dictate selection criteria. A 25% selection intensity ($k=1.27$) among crosses followed by a 5% selection intensity within crosses ($K=1.87$) will give 15 parents for the subsequent cycle of intermating. A restriction on pedigree may be used to maintain genetic diversity, i.e., no more than 4 of the 15 selected crosses can trace to a single parent.

Hill and row plot measures of certain quantitatively inherited agronomic traits in barley are comparable; selection for certain other traits may best be postponed until sufficient seed is available, and the number of lines for observation sufficiently reduced, to allow for row plot evaluation (Tragoonrung *et al.*, 1990). The limited spatial requirements of hill plot evaluation of the 1200 DH lines allows for the desirable simplicity of a randomized complete block (RCB) design. A restricted randomization, i.e., a sets-in-replicates, would be appropriate if larger plots are used.

DHRS based on a CPD mating is manageable in terms of crosses and evaluation procedure, and it fits

cyclic selection (25% selection among crosses and 5% selection among lines within a cross). Despite the large number of entries in this experiment, the simplicity of an RCB is more attractive than the restricted randomization alternatives. With hill plot evaluation, total space requirements will be minimal. Alternative selection procedures offered by Gallais (1988) are of interest and merit testing. Important issues are the relative importance of additive \times additive epistasis and the balance of among cross vs. within cross selection. We have synthesized a C0 winter barley DHRS population derived from a CPD mating and will use it for the improvement of resistance to biotic and abiotic stresses.

MSFRS populations offer an alternative approach to doubled haploid recurrent selection, and I offer the following scheme for your consideration. It is designed to capitalize on the MSU/ICARDA MSFRS populations in the context of germplasm enhancement for the West Asia/North Africa (WANA) region. This is essentially a modified ear-to-row system that is designed to simultaneously: (1) maximize gain from selection in the MSFRS populations; and (2) derive inbred lines for parental stocks, release as varieties, or components of "synthetic landraces."

Cooperators at targeted locations would select male fertile plants from the MSFRS population. Selections would be assigned identifiers and reserve seed maintained. DH lines would be extracted from each selection. Assuming the frequency of msms genotypes in the source population was 25%, the frequency of male fertile doubled haploids will be 66%. DH lines would be evaluated at each targeted location. The MSFRS population would be re-synthesized from reserve parental seed of superior DH lines, while cooperators at each location would select DH lines for immediate increase and further evaluation.

Since many of the barley varieties grown in the stress environments of the WANA region are landraces — the term landrace being defined as a population of genotypes of a particular crop species that have evolved in a particular regional cropping system (Harlan, 1975) — there is considerable merit in exploring the use of DH lines to mimic the advantages of traditional landrace heterogeneity.

In dry and marginal areas, those at which development efforts are most appropriately targeted, landraces are more stable and often higher yielding than pure-line cultivars. In such environments, consistent performance is more critical than occasional

outstanding performance. The advantage of landraces over pure-line genotypes is attributed to a "buffering effect" (Allard & Bradshaw, 1964) that may be due to both heterogeneity and heterozygosity.

The heterogeneity of Middle East landraces for a range of qualitative and quantitative traits has been elegantly documented. Weltzien (1988, 1989) has demonstrated that intra-population variation for both qualitative and quantitative agronomic traits in Syrian and Jordanian landraces is often greater than inter-population variation. A similar wealth of intra-population diversity has been found for landraces from Nepal and Yemen (Damania *et al.*, 1985) and Ethiopia (Bekele, 1983, 1984). An abundance of within-population variation for resistance to a number of fungal pathogens in Syrian and Jordanian landraces was found by van Leur *et al.* (1989).

Given the wealth of evidence supporting landrace diversity and stability of performance, researchers dedicated to barley improvement for marginal stress environments have concluded that such materials are: (1) a source of valuable parental material for crossing programs directed at developing genotypes appropriate for stress environments; and (2) that multi-component mixtures, or "synthetic landraces," may be more appropriate than pure-line cultivars for such environments (Weltzien, 1988; van Leur *et al.*, 1989).

Successful exploitation of the genetic resources found in landrace populations and the development of synthetic landraces capable of providing consistently more stable and higher returns to producers in marginal stress environments requires the development of a rapid and efficient breeding system for exploiting crosses of landrace genotypes *inter se* and with exotic germplasm sources, as well as a systematic approach to development of synthetic landraces. DH lines meet these criteria, providing an ideal vehicle for germplasm introgression, enhancement, and development of multi-component mixtures.

Cultivar mixtures have been shown to reduce disease severity in cereals by reducing the rate of epidemic development, since any given race of the pathogen will be virulent on only a portion of the plants in the mixture. The findings of van Leur *et al.* (1989) regarding disease resistance in Syrian and Jordanian landraces confirm results found in multi-component mixture trials (Frey *et al.*, 1973; Wolfe & Barrett, 1980). Field studies of multi-component mixtures for control of barley scald (induced by *Rhynchosporium secalis*) indicate a decrease in disease, as well as an increase in yield performance

attributable to mixing *per se* (Schon & Hayes, 1989).

Population buffering (Allard & Bradshaw, 1964) and heterogeneity are documented to increase and stabilize yields of small grains in landraces (Ceccarelli & Grando, 1989) and multi-component mixtures (Nitzsche & Hesselbach, 1983). The key in capitalizing upon the advantages conferred by mixing lies in identifying optimum mixture components. Extrapolating from the combining ability concept, Gizlice *et al.* (1989) present models for identifying genotypes that perform well across two-way mixture combinations (General Mixing Ability) and genotypes that respond in specific mixtures (Specific Mixing Ability). Federer (1979) recognized the limitations of diallel-type analyses and presented models for analyzing mixtures of any number of cultivars. Finally, Griffing (1989) has presented a group gene model describing complexities inherent in plant mixtures. We are currently researching the synthesis of synthetic landraces. Field evaluation provides an opportunity to implement and validate current mixture theory to the very real benefit of small farmers in the WANA region.

An exciting application of DH lines, and one that unifies disciplines of quantitative, molecular, and classical genetics, is quantitative trait locus (QTL) mapping. As this topic is the subject of Dr. Tom Blake's presentation ("Modern Mapping Methods for Genome Analysis"), I will provide only a brief overview of QTL mapping activities and the benefits afforded by DH lines. F1-derived DH lines are of particular utility in this context because they provide an immortal reference population allowing for simultaneous linkage map construction and trait evaluation. Furthermore, DH lines, as opposed to other genetic reference populations, provide computational efficiencies in the QTL analysis process.

My research group is currently involved in two QTL mapping projects: the North American Barley Genome Mapping Project (NABGMP) and a cooperative effort with Dr. Blake to map QTLs associated with cold tolerance. The underlying rationale in these two projects is the same: Many, if not most, important characteristics of agricultural species are inherited quantitatively. Of necessity, genetic analysis of such traits has been approached with biometrical procedures. While progress in the improvement and understanding of quantitative traits through conventional biometrical procedures is impressive, even greater efficiencies may be realized by using Mendelian markers to map and select for quantitative traits. Whether the linkage of quantitative trait effects will be

major genes, isozymes, or RFLPs (Lander & Botstein, 1989), the intent is to reduce the complexity of quantitative characters to the simplicity of Mendelian analysis.

Objectives of the NABGMP are to: (1) construct a comprehensive, high-density barley genome map (10 centimorgans between markers) using restriction fragment length polymorphism (RFLP) and isozyme markers in doubled haploid populations; (2) use the map to identify and locate genes and quantitative trait loci (QTL) controlling economically important traits including those for adaptation, pest resistance, yield, and malting and nutritional quality; (3) provide the basis and framework for a program of barley varietal development by design; (4) generate new knowledge about barley genome evolution and structure and provide the basis for genetic engineering of economically important traits; and (5) establish a cooperative mapping project ranging from molecular genetics to breeding that will be a functional and organizational model for the cereals and other crop plants.

We have produced over 300 DH lines from each of two crosses: Steptoe X Morex and Harrington X TR306. For each cross, 150 DH lines will be used for simultaneous map construction, trait evaluation, and QTL analysis. These DH populations will provide immortal reference populations — seed will be maintained in the United States National Small Grains Germplasm Collection — for current and future mapping activities.

Map construction is straightforward using available mapping software (i.e., Mapmaker; Lander *et al.*, 1987), and further streamlined by the completely inbred nature of the DH lines. QTLs are identified through a synthesis of the linkage map and field performance data. Knapp *et al.* (1990) have presented a flanking marker genetic model for DH progeny. The model is a function of the means of quantitative trait locus genotypes and recombination frequencies between marker and quantitative trait loci. A key component of the NABGMP is extension of this model to investigate QTL locus effects in different environments. Thus, contrasts can be specified for estimating additive effects, additive x additive effects, and the interactions of these effects with environments. The populations of DH lines provide a vehicle for actually exploring the genetic basis of genotype x environment interaction.

The immortality of the DH mapping population also allows for a synthesis of QTL analysis and classic quantitative genetics. Knapp and Bridges (1990) have described how power for testing hypotheses

about QTL genotypes is affected by the number of replications per DH line (r), and the number of replications of QTL genotypes (n). Estimation of QTL effects alone is maximized by minimizing r and maximizing n . Assuming the DH population represents a random sample of gametes, in a population of 150 DH lines there are 75 replicates of any given QTL locus. Fractional replication of some portion of the total DH population, say 50 lines, simultaneously allows for estimation of pertinent genetic variances. The genetic variance between lines nested in QTL genotypes is the fraction of the genetic variance between lines that is not accounted for by intralocus and interlocus QTL parameters.

As stated at the outset, the issue in barley improvement today is not how to produce DH lines, but how to use them. *H. bulbosum*-mediated chromosome elimination, using *in vitro* floret culture, provides a simple, straightforward approach to DH production appropriate for laboratories with minimal infrastructure and tissue culture expertise. DH lines developed by this method have been shown to represent random samples of F₂ gametes and are therefore appropriate for linkage analyses and breeding activities intent upon capitalizing on sexual variation. Considerable strides have been made in androgenetic DH production and the potential efficiencies of these approaches are far superior to those achievable through the bulbosum technique. However, it remains to be shown that androgenetic DH lines are not subject to gametophytic selection and/or culture induced variation.

DH lines promise to accelerate and increase the efficiency of recurrent selection based on MSFRS and/or systematic matings. An evaluation of DH lines for germplasm introgression via the systematic mating of a circulant partial diallel is underway. DH lines promise to increase the efficiency of MSFRS as a tool for international germplasm enhancement. DH lines are an ideal vehicle for analysis of landrace populations and the production of "synthetic landraces" based on multi-component mixtures. Finally, DH lines provide the immortal genetic reference populations required for quantitative trait locus mapping through simultaneous linkage analysis and quantitative trait measurement.

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Using Genetics in Barley Breeding

Thomas K. Blake and Nancy Lybeck*

Introduction

Many of the problems facing plant breeders have faced agriculturalists for thousands of years. Plant breeding theory rests on a limited number of relationships. Genetic gain per generation is dependent on the availability of genetic variance, effective selection techniques, and an acceptable population mean. Effective selection requires both reasonable heritability and a sufficiently large population. Breeders disagree about the relative difficulty each parameter poses. Some breeders do their best to maintain populations which contain enormous genetic variance; these breeders generally have populations which contain a few exceptional individuals but which in composite look terrible in the field. Other breeders make crosses between closely related lines, and find progeny which, although essentially identical to their parents, occasionally outperform them in one or more characters. Still a third group of breeders spends a great deal of effort working with characters with low heritabilities. These project leaders measure variation among enormous numbers of lines derived from populations. Plainly, points of balance among these parameters are found by each plant breeder; these points of balance are commonly referred to as the "breeder's philosophy."

One of the problems facing the barley breeding program in Montana is the absolute need to maintain and improve grain quality. While barley varieties are available which show exceptional yield potential over much of Montana (Steptoe is one example), our market demands the high grain quality found in the 2-rowed varieties recommended in the state. When a breeder makes a cross between lines like Hector and Clark, all the progeny look essentially like Hector and Clark. We find very little variation for straw strength, yield potential, or disease resistance. We must be able to move genes controlling characters like these from parent lines like Steptoe into varieties like Clark without losing the needed quality.

Currently, the best approach for accomplishing this task is to use the tools of molecular biology to "mark" the genes we want to transfer from poor quality varieties into our high quality recommended

varieties. Plant breeders have been trying to do this for over 50 years, and with a technique called "restriction fragment length polymorphism" (RFLP) analysis, we are beginning to have success. We have been able to locate genes which modify characters ranging from yield and kernel weight to genes controlling plant height, when the plant flowers, and how hot the plant becomes when the grain is filling. Figure 1 shows the location of some of the genes we have identified which modify plant height, flowering date, and kernel weight.

Methods

Identification of Molecular Variation

Brown and Weir (1983) surveyed isozyme variation in cultivated barley and *Hordeum spontaneum*. The limited isozyme variation which was identified suggested that other types of molecular variation would be needed if marker assisted selection is to be generally useful. Several workers utilized the *Hor-1* and *Hor-2* loci to mark resistance alleles to powdery mildew (for example, Hasn *et al.*, 1982), but due to a shortage of readily available markers which were linked to agronomically significant genes, the impact of marker assisted selection has been quite limited in barley.

Traditional restriction fragment length polymorphism (RFLP) analysis requires the generation and screening of genomic or cDNA clones against blotted restriction endonuclease digests of DNA from accessions of the target species. So little molecular level was found in cultivated tomato (*Lycopersicon esculentum* L.) that interspecific crosses were utilized in initial map construction (Bernatzky & Tanksley, 1986). An initial survey of cultivated barley germplasm (Shin, 1989) found that approximately half the cDNA clones tested and about one-third of the low copy number genomic clones evaluated identified structurally different alleles among barley cultivars.

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While barley evinced less diversity than maize (Helentjaris *et al.*, 1985), it appeared that enough variation was available to make map construction feasible within agronomically informative crosses. An initial map was constructed (Shin *et al.*, 1990) and markers placed on a map anchored to chromosomes by 10 previously mapped morphological marker loci.

Identification of Quantitative Trait Loci

One hundred F_2 plants were utilized to construct the map, and F_4 and F_5 bulks from each plant were utilized as test populations to permit the identification of QTLs. Line means over years were evaluated over genotypes for each locus at which genotype was determined using the GLM procedure of SAS. Significant effects are shown as LoD scores, which are defined as the negative base 10 logarithm of the p-value (Figure 1).

Results and Discussion

Single Locus Effects

One of the first applications of our findings was the development of an understanding of the relative heritabilities of the characters we measured. We are now quite certain that a substantial portion of the measurable variance among lines for plant height, flowering date, yield, canopy temperature, kernel weight, and protein content can be attributed to segregation at a very limited number of loci. Plant breeding is an historical process, and undoubtedly genes of low breeding value have been fixed within our elite germplasm pools. Identifying and eliminating these from our best germplasm resources will provide the next predictable dramatic source of improvement in our next generation of released varieties.

Multiple Character Effects

Some of the loci monitored appeared to have interactions with more than one of the characters evaluated. The peroxidase alleles from the 6-rowed parent in this cross were associated with taller and later plants with smaller kernels. Similarly, multiple effects were observed with phosphogluconate dehydrogenase, xMSU51, and *s*. While essentially impossible to distinguish between tightly linked independent QTL loci and pleiotropy, the result to the breeder is basically identical. The genes associated with the peroxidase alleles from the 6-rowed parent were associated with extreme earliness, reduced stature, and low kernel weight. In 1989, we also found this

interval to be associated with low yield (data not shown). Unless extreme earliness was desired, selection for the peroxidase alleles from the 2-rowed parent would be an obvious recommendation.

Evaluation of Genes with Known Effects

A few of the morphological marker loci segregating in lines evaluated in this experiment showed predictable effects on characters. The *v* locus, which is a primary determinant of headtype, had a significant effect on kernel weight. Six-rowed heads (*vv*) had kernels on average 7 mg (20%) lighter than 2-rowed heads. The *n* locus, which determines whether the lemma and palea are adherent, also had an obvious effect on kernel weight. Hulless (*nn*) barleys showed kernel weights approximately 3 mg lighter than their covered counterparts (about 10% of the grain is accounted for by the lemma and palea). Surprisingly, *wst,,b* had little effect on most characters. The phenotype, white striping on leaves of secondary tillers, would seem decidedly undesirable. However, the QTL associated with this gene confers only moderate lateness, increased kernel weight, and slightly increased stature (Figure 1).

General Conclusions

The only way to estimate the heritability of a character is through replication of lines. The only way to determine if there is a genotype by environment interaction for a character is to replicate lines within environments and experiments over environments. Nonetheless, the number of lines in an analysis appears to have a significant effect on the sensitivity of an analysis. As Knapp and Bridges (1990) suggested, an important parameter relating to the importance of population size is the ratio of the effect of the gene being analyzed to the effects of other genes segregating in the cross which also have an effect on the character. While replication within an environment is not necessary for identification of gene by character interactions, it is probably still a generally good idea. Map saturation is expensive, time consuming, and does not appear necessary for identifying the effects of single genes on characters. However, it is a good investment of effort if accuracy is important in estimating the phenotypic effect of a gene. Recognizing the limitations of extensive field analysis, a compromise should be reached between the need for as large a number of lines in the field as possible, and the need for replication. Partial replication may form a part of this compromise.

One obvious problem involved in this analysis was the use of bulks from F_2 individuals. As previously reported (Blake *et al.*, 1989) it is much easier to identify the performance of an inbred line than a segregating population. Burr *et al.* (1988) recommended the use of recombinant inbred lines in mapping and QTL programs, and we find that advice sound. Recombinant inbreds are much more homogeneous than bulks, and are therefore easier to maintain. They are also essentially immortal and can be easily shared among projects.

Paterson *et al.* (1990) demonstrated the value of marker assisted selection for major genes affecting solids content in tomatoes. While backcrossing is not the approach of preference for most practicing plant breeders, the identification and use of markers associated with desirable and undesirable alleles at developmentally significant loci has obvious value.

Coming back to breeder's philosophy, if we can describe the effects of genes which have major developmental consequences (for example, the Per1-Per2 interval), we may be able to avoid unwanted transgressive segregation in populations we actually evaluate. By making wider crosses less risky and more productive, we may put plant breeding on a less "philosophical" and more material basis, and we might even avoid the germplasm bottlenecks we seem to be approaching in many of our field crops.

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1988-1989 QTL DATA ANALYSIS

GENOTYPES REGRESSED ON LINE MEANS

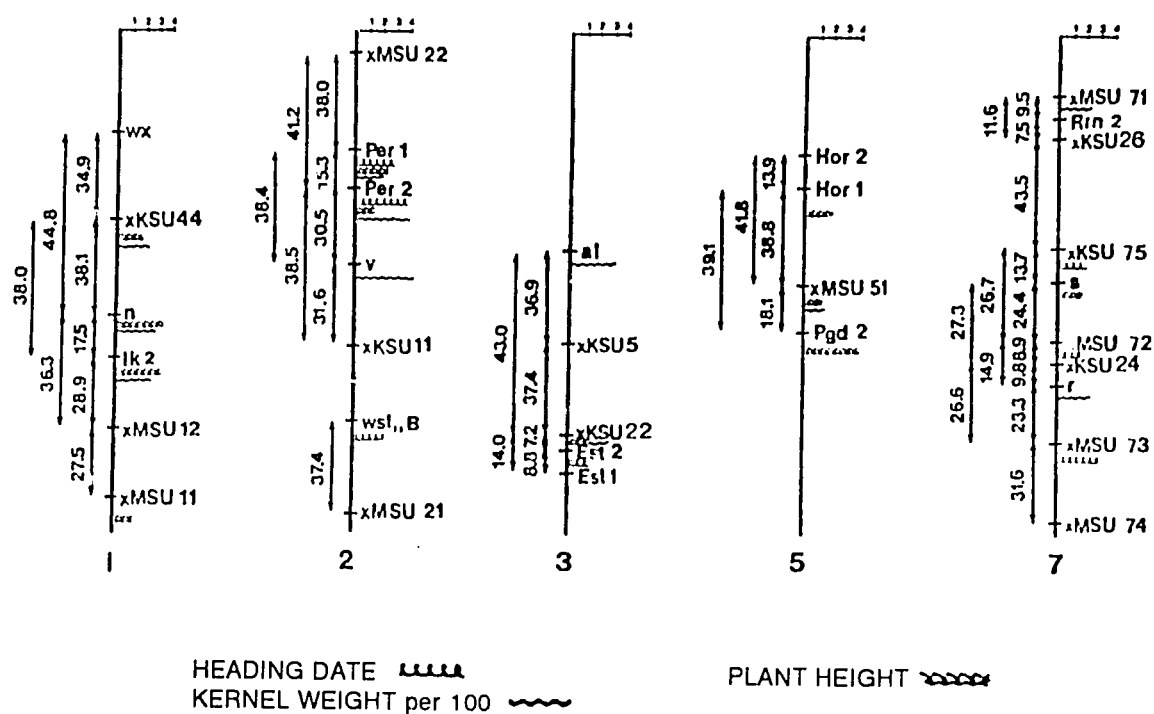


Figure 1. Location and LoD scores for genes showing interactions with plant height, flowering date, and kernel weight over 2 years.

Potential for Transformation in Barley

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Introduction

Stable genetic transformation conferring heritable expression of an exogenous DNA sequence will very soon be a reality in all cereals including barley. Substantial progress has been achieved in several aspects of cereal transformation research. Improvements in DNA delivery methods, cell and tissue cultures, and selection systems for recovery of transformed cereal cells or plants have been reported. Plants have been regenerated from protoplasts of rice (Fujimura *et al.*, 1985; Abdullah *et al.*, 1986; Toriyama *et al.*, 1986; Yamada *et al.*, 1986), maize (Rhodes *et al.*, 1988; Prioli *et al.*, 1989; Shillito *et al.*, 1989), and wheat (Vasil *et al.*, 1990). Transformation has been reported in rice (Shimamoto *et al.*, 1989; Hayashimoto *et al.*, 1990) and maize (Rhodes *et al.*, 1988) using protoplasts as target cells for direct DNA uptake. More recently, the development of particle acceleration technology for DNA delivery into intact cells has obviated protoplasts as targets for transformation and has simplified the tissue culture requirements for cereal transformation. Accordingly, tobacco (Klein *et al.*, 1988c), soybean (McCabe *et al.*, 1988), and maize (Gordon-Kamm *et al.*, 1990) have been transformed using particle acceleration. The objectives of this paper are: (1) to review the current status of the requisite components of barley transformation systems, and (2) to compare the progress in barley to transformation research with other cereals.

Identification of Totipotent Cells as Targets for DNA Delivery

Introduction of DNA into the developing zygote in planta represents an ideal transformation strategy because the zygote is inherently totipotent and tissue culture would not be required. Bypassing tissue culture in a transformation protocol would minimize genotypic specificity associated with successful initiation of regenerable tissue cultures of barley and the deleterious somaclonal variation associated with tissue culture. Furthermore, if DNA integration occurred simultaneously with fertilization, resulting

transgenic plants would be uniformly transformed in both somatic and germline cells.

Reports of successful cereal transformation via DNA delivery to the developing zygote include using DNA treatments of pollen, developing microspores of rye (De La Pena *et al.*, 1987) and barley (Mendel *et al.*, 1990), and barley stigma shortly after pollination (Mendel *et al.*, 1990). These results are extremely promising but as yet are not widely corroborated, indicating that they are not yet routine. Furthermore, they are labor and space intensive, as exemplified in a recent report by Mendel *et al.* (1990). DNA was macroinjected into floral tillers of 2055 plants and DNA was applied to stigmas of 1058 plants 5-20 minutes after pollination. The frequency of kanamycin-resistant selectants among a total of ca. 40,000 seedlings screened was about 10^{-3} to 10^{-4} for both approaches. The appropriate DNA fragments were detected by Southern blots of the transformants and their progeny; however, expression of neomycin phosphotransferase could not be detected in the putative transformants or their progeny. Transformation of pollen using particle acceleration prior to pollination seems to be an attractive approach to directly transform the germline. However, further research is required to optimize DNA delivery through the tough pollen cell walls while maintaining pollen viability. Immature zygotic embryos also would appear to be good targets for DNA delivery. Transformed rape-seed plants have been regenerated from microspore-derived (somatic) embryoids microinjected with DNA (Neuhaus *et al.*, 1987). However, successful application of this approach to cereals has not been reported. This may be because the few germline cells in a cereal embryo are difficult to transform by microinjection. Particle acceleration-mediated DNA delivery into immature zygotic soybean embryos followed by a limited tissue culture step yielded stable transformed

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plants (McCabe *et al.*, 1988). However, similar attempts to transform immature zygotic cereal embryos have not resulted in transformed plants. Many of us, especially those involved in cereal tissue culture development for transformation, eagerly await further corroboration and optimization of whole plant transformation systems.

Cell cultures offer certain advantages over some whole plant transformation approaches. Foremost among these are the very large numbers of totipotent target cells (10^7 to 10^8) that can be treated to take up DNA in relatively small and simple experiments involving direct DNA uptake into protoplasts or particle acceleration into cells. A further advantage is that tissue cultures enable efficient selection of transformed callus based on a substantial body of literature on transformation of nonregenerable cereal tissue cultures.

DNA Delivery Methods

Cereal cells exhibit limited susceptibility to *Agrobacterium*, the mainstay of dicot transformation. Delivery of DNA into cereal cells by *Agrobacterium* was first demonstrated by Agroinfection of maize with a T-DNA vector carrying maize streak viral DNA causing a systemic infection (Grimsley *et al.*, 1987). However, barley and other cereals, including maize, apparently are not sufficiently susceptible to infection by *Agrobacterium* to warrant its use as an efficient transformation vector in tissue cultures. Recently, Brettschneider *et al.* (1990) reported that application of *Agrobacterium tumefaciens* to barley flowers at anthesis resulted in a few seedlings carrying the appropriate exogenous DNA sequence. Further analyses of these putative transformants were not reported.

Direct DNA delivery (nonvector) methods may be subdivided into methods for delivery of DNA into protoplasts and cells. The plasma membrane surrounding the protoplast is easily modified to allow DNA and other macromolecules to be taken up by the cell. DNA uptake by protoplasts and successful transformation can be mediated by chemical treatments, as most recently demonstrated in rice (Hayashimoto *et al.*, 1990), and by electroporation (Fromm *et al.*, 1986). Both techniques result in high frequencies of transient gene expression and stable transformation of colonies cultured from the treated protoplasts and regenerated plants. Recently, regeneration of barley plants from protoplasts has been reported (Lazzeri & Lorz, 1990). However, routine protoplast to plant culture systems is not widely reported in barley. Further

discussion of the advantages and disadvantages of protoplast cultures will be presented below.

Introduction of DNA into intact plant cells has been accomplished using microinjection, particle acceleration, and vortexing in the presence of silicon fibers. Of these procedures, particle acceleration has become the method of choice primarily because the procedure can be used to routinely deliver DNA into large numbers of intact cells ($>10^3$ per shot in some cases) that retain viability after treatment. In contrast, microinjection has limited applicability because of the low numbers of cells that can be injected over time. To date, soybean (McCabe *et al.*, 1988), tobacco (Klein *et al.*, 1988c), maize (Gordon-Kamm *et al.*, 1990) and, in preliminary reports, barley (Mendel *et al.*, 1990) have been transformed using particle acceleration.

Optimization of DNA delivery by particle acceleration is dependent on the quality of preparation of DNA-coated tungsten or gold particles, ballistic parameters such as acceleration distance and evacuation of the firing chamber, and target cell type (Klein *et al.*, 1988b). In oats we have optimized these parameters so that transient expression of a β -glucuronidase (GUS) reporter gene routinely exceeds 100 events per shot, whereas, in a maize suspension culture, we achieve >1000 events per shot routinely. Conditions for optimal frequencies of DNA delivery differed for oat and maize in our hands; thus it seems likely that the conditions for DNA delivery into barley cells will have to be empirically determined. As mentioned, conditions for delivery of DNA via microprojectiles into barley suspension culture cells have been described (Mendel *et al.*, 1989).

Recently, we have been investigating using silicon carbide fibers to mediate DNA delivery into intact cells. This procedure is a modification of procedures developed by Dr. Andrew Cockburn, USDA-ARS, Gainesville, Florida, for DNA delivery into insect eggs. Maize cells from a nonregenerable suspension culture were vortexed in the presence of the silicon carbide fibers and GUS DNA (Kaeppler *et al.*, 1990). Transient expression of GUS activity was routinely observed at an estimated frequency of 10^{-5} . Although this frequency of DNA delivery is probably 10 to 100 times lower than particle acceleration-mediated DNA delivery, this method deserves further investigation because of its low cost and rapidity. The only apparent drawback is that the silicon carbide fibers are carcinogenic.

Successful transformation of fertile cereal plants inevitably depends on the combination of efficient

DNA delivery followed by selection of transformants and regeneration of plants from transformed tissue cultures. The primary limitation to transformation of cereals appears to have been the identification of appropriate tissue cultures. For example, particle acceleration was first reported in 1987 (Klein *et al.*, 1987). Its application to maize cells was reported one year later by Klein *et al.* (1988b). Nonregenerable cells were transformed in the following year (Klein *et al.*, 1989), and it was not until the third year after the initial report that fertile transgenic maize plants were reported (Gordon-Kamm *et al.*, 1990). Although regeneration from maize tissue cultures was widely reported before 1986, improvements in tissue cultures and most importantly regenerable suspension cultures were key developments leading to the recent success (Gordon-Kamm *et al.*, 1990). Therefore, it seems likely that improvements in barley tissue cultures will be required before routine transformation systems can be developed.

Barley Tissue Culture

Major factors influencing tissue culture initiation and plant regeneration are choice of explant for culture initiation, explant genotype and its physiological status, as well as culture medium and environment. Barley is typical of cereals in terms of its tissue culture response to a number of these factors. Regeneration of plants from barley tissue cultures was first reported in 1975 (Cheng & Smith). A partial listing of the different genotypes, explants, and differentiation modes of diploid barley tissue cultures is presented in Table 1. A similar list of haploid tissue cultures is presented in Table 2. These tables indicate that substantial effort has gone into the development of barley tissue cultures and illustrate that explant and genotype influence the ability to establish regenerable tissue cultures. Response to culture medium is exemplified in Table 3, illustrating the effect of 2,4-D concentration on tissue culture initiation. Factors such as carbon source have been shown to have significant effects on haploid culture initiation, as recently reviewed by Kasha at the 1989 Stadler Symposium. Initiation of regenerable suspension cultures (Luhers & Lorz, 1988) and plant regeneration from protoplasts isolated from these suspensions (Lazzeri & Lorz, 1990) have recently been reported. These results indicate that it is possible to establish dedifferentiated but totipotent cell cultures of barley similar to the cultures of maize that have been transformed via particle acceleration.

A major problem in barley seems to be the maintenance of callus or suspension cultures in a nondifferentiated state while retaining plant regeneration. Only one report of long-term regeneration (>3 years) (Weigel & Hughes, 1985) was found in the literature for this review. Long-term retention of plant regeneration is essential to allow establishment of dedifferentiated tissue cultures and selection of transformed callus following DNA delivery. In the case of transformed maize plants reported by Gordon-Kamm *et al.* (1990), the suspension cultures were 4-5 months old (callus age not reported) before bombardment. After bombardment, selection was carried out for 6 to 7 weeks prior to plant regeneration. Extending these results to barley, plant regeneration capacity must be retained for longer than 6 to 7 months following callus establishment. Luhers and Lorz (1988) reported regeneration of only albino plantlets from barley suspension cultures, indicating that continued improvements are required to extend the regenerability of barley tissue cultures.

For use in transformation studies, there are no major advantages of haploid tissue cultures over regenerable diploid tissue cultures because transformation marker genes are dominant. However, the shed microspore cultures recently described by Kasha *et al.* (1990) are appealing target tissues for particle acceleration-mediated transformation. Microspores shed from cultured anthers are single-cell explants that convert to somatic embryos and eventually plants. DNA could be introduced by particle acceleration into the microspores in the intact anther or following shedding into the culture medium. Even though microspore-derived colonies may be multicellular once shed, selection would allow only transformed cells to proliferate to form uniformly transformed regenerable structures. The major advantage of microspore cultures as target cultures for transformation is the possibility of introducing DNA into the explant shortly after culture initiation, thereby reducing the tissue culture phase and maintaining good plant regeneration capacity as opposed to establishing the appropriate target tissue cultures from multicellular explants such as immature embryos. However, it is likely that barley microspore cultures are limited to specific high responding genotypes as observed for anther cultures.

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TABLE 1. Genotypes and explant source of diploid barley tissue cultures capable of plant regeneration.

GENOTYPE	TISSUE SOURCE	REGENERATION	REFERENCE
Himalaya, Mari	Apical meristem	Organogenesis	Cheng & Smith, 1975
Coho X <i>H. jubatum</i>	Immature ovary	Organogenesis	Orton, 1979
Akka, Asse, Butte, Georgie, Klages, Mazurka, Pirolina, X2387-3	Immature embryo	Organogenesis	Hanzel <i>et al.</i> , 1985
Akka, Advance, Apam Dwarf, Benton, C2-79-198, Diamant, Gus, Karl, Klages, Mex 79132-Hk, Minn 66-102, Morex, Multum, OR 7334-3, ORSS-2, OSD 763390, Short Wocus, Steptoe, Triumph	Immature embryo	Organogenesis	Goldstein & Kronstad, 1986
Atlas	Apical meristem	Embryogenesis & organogenesis	Weigel & Hughes, 1985
Akka, Armelle, Mazurka	Immature embryo	Organogenesis	Dale & Deambrogio, 1979
F4 line of 4.36/3	Mesocotyl	Organogenesis	Jelaska <i>et al.</i> , 1985
Maxima	Mature embryo	Organogenesis	Lupotto, 1984
<i>H. bulbosum</i> , <i>H. spontaneum</i>	Immature embryo	Organogenesis	Breiman, 1985

TABLE 2. Barley genotypes capable of plant regeneration from haploid tissue cultures.

GENOTYPE	TISSUE SOURCE	REGENERATION	REFERENCE
Betzes, Bruce, Klages, Perth, Trent	Immature embryo	Embryogenesis	Seguin-Swartz <i>et al.</i> , 1984
Frigga, Plena	Apical meristem	Organogenesis	Saalbach & Koblitz, 1977
Bruce, Klages, Perth, York	Immature embryo	Embryogenesis	Kott & Kasha, 1984
Coho X H. jubatum	Immature ovary	Organogenesis	Orton, 1980
Elrose	Anther	Embryogenesis	Marsolais & Kasha, 1985
Sabarlis	Anther	Embryogenesis	Powell <i>et al.</i> , 1984
Akka, Sabarlis	Anther	Organogenesis	Clapham, 1973
Bonanza, Elrose, Jet	Anther	Embryogenesis	Kao, 1981
28 F1 hybrids, 33 parents	Anther	Embryogenesis	Friedt & Foroughi-Wehr, 1983

TABLE 3. Frequency of tissue culture initiation for different genotypes of barley.*

GENOTYPE	2,4-D (mg/L)		GENOTYPE	2,4-D (mg/L)	
	1	2		1	2
Akka	75	63	Morex	58	55
Mazurka	18	35	Larker	0	0
SD77-163	65	30	Hazen	0	0
X2387-3	53	68	Azure	0	0
Robust	5	38			

*Embryos (1.2 and 1.6 mm long) were isolated from immature kernels 7 or 8 days after anthesis and cultured on MS media containing 1 or 2 mg/L 2,4-D. (Unpublished data from X. Wu, B. Gengenbach, & D. Rasmussen.)

Montana-USAID Activities in Developing Barley Germplasm

Michael E. Bjarko*

Today I will talk about the barley development activities of the cooperative project between Montana State University and the Agency for International Development. This presentation does not cover the substantial amount of barley breeding work being carried out by Dr. Tom Blake at Montana State University or by Dr. Gene Hockett with the USDA.

I am no longer involved with the Montana-USAID Project. I am now the barley breeder for Busch Agricultural Resources, Inc., a subsidiary of Anheuser-Busch. However, my presentation deals with the research I performed while I was with the Project, particularly the work I did as a postdoctorate.

I have been involved with the Montana-USAID Barley Project in a number of capacities: from 1976 to 1979 as a graduate student at MSU, in 1979 and 1980 as a research associate with ICARDA, in 1981 and 1982 as a research technician with Professor R.F. Eslick, and from 1987 to August of 1989 in a postdoctorate position with Dr. Dave Sands. I have had the opportunity to observe the Project evolve and develop from different perspectives and over a number of years.

The Montana-USAID Barley Development Project has been in existence for 16 years. The approach taken by the Project has been to utilize male sterile facilitated recurrent selection as a breeding approach in developing barley germplasm for developing countries (Bockelman & Sharp, 1986; Sharp, 1983). Over the past 16 years the Project has undergone several changes, evolving into the program it is today.

The Project had three objectives when it was initiated in 1974 (Carter, 1977): (1) to increase the nutritive value of barleys consumed by people throughout the world, (2) to increase the yield of barley grown in semi-arid regions of the world, and (3) to decrease losses caused by barley diseases. All three of these objectives were targeted particularly toward the lesser developed countries.

The Project began to develop male sterile facilitated recurrent selection populations (MSFRSPs) in order to attain these goals. These populations were initiated by Professor Robert F. Eslick. Populations

were developed to select for seed plumpness, earliness, drought tolerance, and disease resistance. The diseases given initial attention were scald, net blotch, and covered smut. The populations developed for disease resistance were developed primarily by Drs. H.E. Bockelman and E.L. Sharp, using the methods of R.F. Eslick (1977) and R.T. Ramage (1977).

In 1977, the emphasis of the Project changed, concentrating on the development of barley germplasm with broad-based multigenic resistance to a number of diseases. By 1986, 17 MSFRSPs were developed, addressing nine diseases of barley. Seven of these MSFRSPs were eventually registered in *Crop Science* as germplasm sources (Table 1).

These MSFRSPs were developed utilizing a strategy with two cycles: (1) selection of male fertile, disease resistant plants; and (2) genetic recombination (Figure 1). During the first cycle, disease resistant, male fertile plants were selected in Montana. These plants were harvested and the seed was grown in Arizona for the second cycle, that of genetic recombination. During this cycle, natural outcrossing was relied upon to produce seed on male sterile plants, which made up approximately one-fourth to one-third of the population. Only the male sterile plants were harvested, and the resulting outcrossed seed provided the germplasm for the next cycle of selection for disease resistance. During this period of development, a portion of the seed harvested during the cycle of selection for disease resistance was sent not to Arizona, but to a number of locations around the world, particularly in the Middle East and North Africa. At these locations, selection for disease resistance and agronomic adaptation was carried out. This was done in order to expose the MSFRSPs to as wide a range of virulence types of the pathogen as practicable, providing a means for identifying and accumulating multiple disease resistance genes. Seed from these locations was returned to Montana

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and bulked with seed harvested in Montana. The bulk was planted in Arizona to undergo further genetic recombination (Figure 2).

This approach has been successfully used to develop MSFRSPs with disease resistance. Populations developed for resistance to *Rhynchosporium secalis* (scald), *Puccinia hordei* (leaf rust), and *Erysiphe graminis* (powdery mildew) have exhibited significant increases in the percentage of resistant plants in each population when samples of remnant seed from successive cycles were tested simultaneously (Figure 3) (Bjarko *et al.*, 1988; Harrabi *et al.*, 1981; Reinhold *et al.*, 1990). The MSFRSP developed for minor gene resistance to *Pyrenophora teres*, composite cross XLV, has also exhibited increasing resistance with time (Bockelman & Sharp, 1986). Only the MSFRSPs developed for major gene resistance to *P. teres*, composite cross XXXVIII and composite cross XLIII, have not shown improvement (Bjarko *et al.*, 1988).

Until 1987, selection for disease resistance received priority over agronomic quality. This was done to avoid restricting the germplasm base of the MSFRSPs during their initial development. Minimal selection was made for agronomic characteristics such as straw strength, earliness, and height. Selection for agronomically desirable plants was carried out in a number of countries, but incorporation into the main MSFRSP program was limited. Because natural outcrossing was relied upon for genetic recombination, the earliest genotypes were selected against. In the early 1980s, attempts were made to begin selection for agronomic quality as well as disease resistance.

In 1987, the Project's approach to developing the MSFRSPs underwent a fundamental change. Agronomic characteristics were given equal priority to disease resistance. It was felt that the populations contained sufficient levels of resistance to begin selection for agronomically superior plants. Rather than relying on natural outcrossing, directed hand-crosses with selected individuals were carried out. This allowed selection for earliness as well as other agronomic traits. Selection for disease resistance was shifted away from the F1 generation to the F3 generation. Individual male-fertile plants were selected in Arizona, based on agronomic appearance. These individuals were then tested for disease resistance in Montana and the remaining disease resistant selections were grown in headrows in Arizona the following cycle using the thick-thin technique of

Ramage for agronomic evaluation (Figure 4). These lines are then used as male parents in further crossing blocks. Agronomic characteristics receiving particular attention are earliness, straw strength, height, head size, seeds/head, peduncle size, and seed plumpness. The headrows are now being sent to target areas in the Middle East and North Africa for evaluation and identification of superior lines. Agronomically desirable, disease resistant lines from the ICARDA Cereal Improvement Program have been incorporated into the MSFRSPs in order to enhance agronomic quality and maintain a broad genetic base in the populations.

A system is now in place that can allow a dynamic, ongoing development of each population, while concurrently providing an avenue for exploitation of the MSFRSPs via the headrow component of each MSFRSP. The headrow component gives the Project the ability to test individual lines at a number of locations in the Middle East and North Africa simultaneously, thus giving a more reliable indication of the agronomic quality of that material. The Project has moved from a development phase into an exploitation phase. The MSFRSPs can more readily be exploited by the cooperators in the target areas, as headrows selected in a particular area can be moved directly into yield trials the following season. The headrows also provide more genetically stable germplasm for evaluation than individual F2 or F3 plants. Exploitation of the MSFRSPs has been taking place to a significant extent in Tunisia and on a more limited scale in Egypt.

The Project is addressing the relevant biotic challenges to barley as they arise. MSFRSPs are being developed for resistance to *Puccinia striiformis*, causal agent of stripe rust, and *Diuraphis noxia*, the Russian wheat aphid. In addition, the Project is addressing the needs of cooperators. An MSFRSP was constructed using Syrian landraces and adapted cultivars. This population was provided to the Cereal Improvement Program at ICARDA for development and exploitation. MSFRSPs are being used by Tunisian colleagues to initiate village scale barley development programs in Tunisia.

The Montana-USAID Barley Development Project is a dynamic program which has evolved significantly over the past 16 years. This evolution is a continual process that will allow the Project to adapt to the changing needs of barley in the developing countries.

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TABLE 1. Male sterile facilitated recurrent selection populations for broad-based disease resistance registered as germplasm sources in *Crop Science*.

Registration	Resistance to:	Year
CC XXXVI	Scald	1980
CC XXXVIII	Net Blotch	1981
CC XLI	Leaf Rust	1983
CC XLII	Powdery Mildew	1983
CC XLIII	Scald & Net Blotch	1983
CC XLIV	Barley Yellow Dwarf	1986
CC XLV	Net Blotch (minor gene)	1988

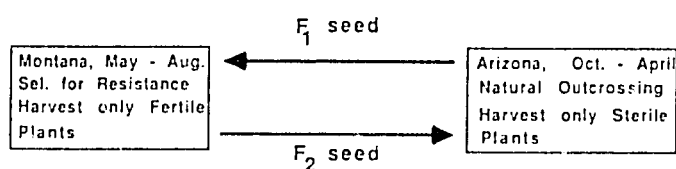


FIGURE 1.

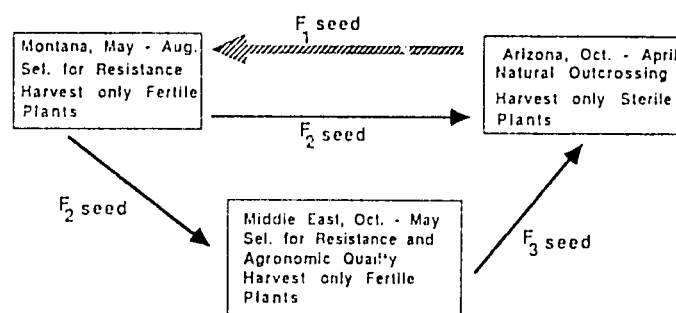


FIGURE 2.

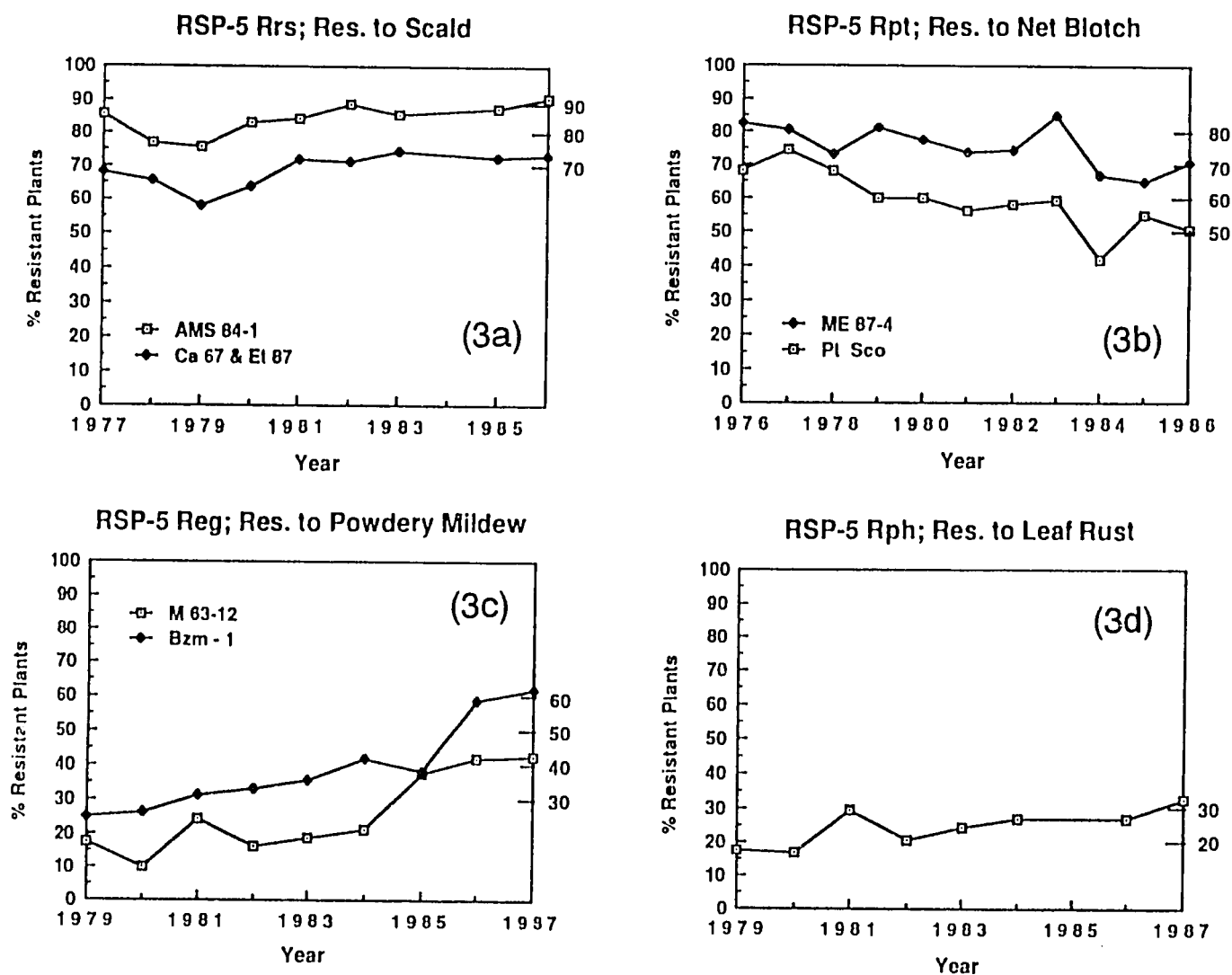


FIGURE 3.

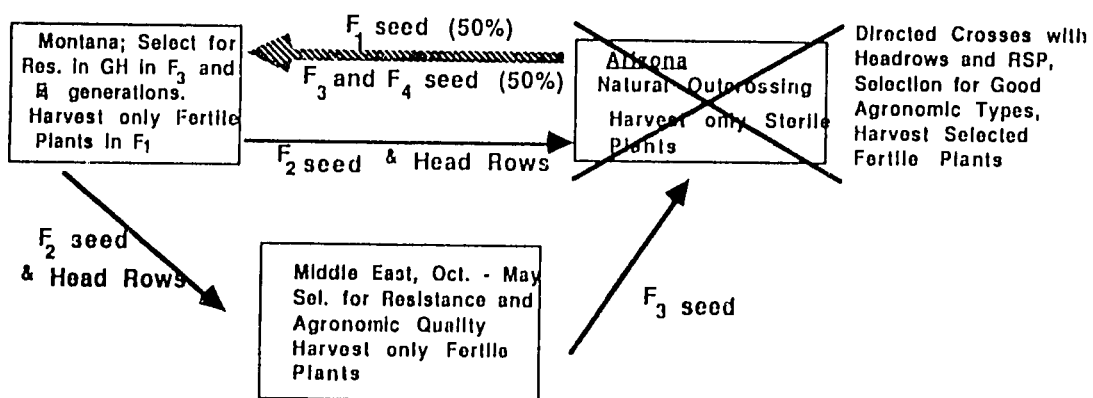


FIGURE 4.

ICARDA Activities in Developing Barley Germplasm

Salvatore Ceccarelli and Joop A. G. van Leur*

Dedication

This paper is dedicated to Dr. A. Zahour, a visiting scientist in ICARDA, responsible for four years of barley breeding for favourable environments, who lost his life in a car accident on July 8, 1990, while on home leave in Morocco.

Summary

This paper describes the activities and strategies in the development of barley germplasm at the International Center for Agricultural Research in the Dry Areas (ICARDA). The presentation includes data on the distribution of barley in less developed countries, the major agroecological environments, the main uses of the crop, and their implications on the structure of the program and on the strategies in developing barley germplasm. The strategies are described with particular reference to the optimum environment for selection, type of germplasm (high input vs. low input varieties, genetic uniformity and genetic variability, landraces and wild relatives), analytical breeding, and diseases and pest resistance.

Introduction

The worldwide importance of barley has been presented already in a previous paper at this symposium. Here we will emphasize only that in the less developed countries (LDC), barley is grown on almost 18 million hectares which represent about 23% of the total barley growing area in the world (Table 1). These nearly 18 million hectares are the target of the activities related to barley germplasm development at ICARDA.

Among developing countries there are large differences in the amount of barley being grown. About 80% of the total barley grown in LDC is grown by eight countries (Table 2). However, in the case of LDC, the area of a crop is not necessarily a good parameter to establish priorities. As an example, the barley growing area in all of the Andean region is about one-quarter of the barley growing area of Morocco alone. Yet, in the social context of the Andean countries, barley is an important staple commodity for 100,000 small farmers' families.

The structure of the barley project at ICARDA, as well as its activities and strategies, is a function of a number of factors: (1) the target environment, (2) the uses of the crop, (3) the farming system, and (4) the interpretation of the role of IARCs in germplasm development.

Target Environments

Unfavourable conditions. Areas where maximum yields, both in experimental plots and in the farmers' fields are low (below 2.0 t/ha), although the causes for low yields are different.

- ▶ Low rainfall/cold winters: Rainfall is typically seasonal (winter), it is less than 300 mm with large year-to-year fluctuations (years with more than 300 mm rainfall have a frequency of 1/25 to 1/40), winters are cold (30 to 60 days with minimum temperatures below 0°C with absolute minimum of -10°C to -15°C), and crop failures are frequent (about four in ten years). Examples are the lowlands in the Middle East and inland areas in North Africa.
- ▶ Similar to low rainfall/cold winters but with mild winters (fewer frost days, and very seldom winter temperatures fall below -5°C).
- ▶ Mountains with continental climate: Very cold and long winters with minimum temperatures as low as -35°C, coupled with low rainfall and low inputs.

Relatively favourable conditions. Areas where total annual rainfall, although variable, is around 350 mm or more, experimental yields are between 5.0 and 6.0 t/ha, farmers' yields are around 3 to 4 t/ha, and both fertilizer and weed control are used. From the point of view of germplasm development, these areas include both winter rainfall environments (crops grown under current rainfall), and summer rainfall environments (crops grown on stored moisture and

*The International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. (Note: Paper presented at Montana symposium by S. Ceccarelli.)

on variable but usually limited amount of current rainfall). In many of these areas, diseases are the most important yield-limiting factor.

Uses of the Crop

In LDC, barley is used as animal feed, human food, and malt.

Animal feed. In large areas of West Asia, North Africa, but also in the Andean countries, in the Himalayan countries, and in China, barley straw — and in many cases both straw and grain — are the major sources of animal feed. The farmers' strategies in these barley growing areas might be difficult to interpret if not considered in a perspective where the animals are the actual agricultural product and not necessarily the crop. Barley is used as animal (mostly small ruminants) feed in a variety of ways which are largely dictated by the environmental conditions:

- ▶ Straw, grain, and stubble after a normal crop harvest.
- ▶ Standing crop at maturity in dry years when the crop is too short to be combined-harvested or, alternatively, hand-pulling if the price of the straw is high enough to cover the labour cost.
- ▶ Winter grazing (before stem elongation): (a) In good years, with large dry matter accumulation during winter, the crop can be lightly grazed by rapidly moving flocks; (b) green forage, i.e., the crop is grown under full or supplementary irrigation, it is clipped, and then is fed to the animals in winter; and (c) in extremely unfavourable years, the crop is fully grazed before stem elongation (this is an example of sacrificing the crop to preserve the animals).

Human food. Mostly in Latin America, the Indian subcontinent, the Himalayan region, the Far East, but also in West Asia and North Africa (WANA), barley is the food of the poor. Also in these areas, straw is an important by-product as covering material and/or animal feed.

Malt. This use of barley is gaining in popularity in a number of LDC (e.g., South America, Ethiopia, Egypt). In China, this is probably the main utilization of the crop.

The Farming Systems

Barley, because of its dependability — especially in unfavourable conditions, is often the only possible crop in low-input agricultural systems. This dependability has induced many farmers (and this is particularly the case in WANA) to crop more and more land to barley and to replace the traditional barley-fallow

rotation with continuous barley to cope with the increased demand for animal feed. This has led to a deterioration of the agricultural land both in terms of fertility and physical structure and to an increased danger of erosion and desertification because of the increased pressure on non-arable land. Because of this, germplasm development at ICARDA, especially for the WANA region, cannot be considered in isolation from other activities which specifically address the issue of sustainability.

The Interpretation of the Role of IARCs in Germplasm Development

An International Center has basically two philosophical choices in germplasm development. The first, which has been the most successful in the past, is based on the development of germplasm that because of photoperiod insensitivity, lack of vernalization requirement, and major gene resistance, is biologically adapted to many latitudes. When a high harvest index is superimposed, a high-yielding variety (HYV) is produced. With this approach, an IARC becomes the major (and often the only) source of germplasm for most national programs. These national programs, in turn, finding it difficult to compete, become totally dependent upon the IARC for germplasm development. An implicit danger of this choice is a dramatic reduction in the genetic variability available within a crop at any moment in time. The second choice is based on the interaction between an IARC and national programs in developing germplasm which is adapted to the conditions (uses, farming systems, environmental stresses) of specific areas. This choice should be equally effective in generating germplasm, it is more effective in maintaining genetic diversity, and it is more effective in improving the research capabilities of national programs. We also believe that an important objective of an International Center is to develop cost-effective methodologies to improve the efficiency of national breeding programs often limited by scarce resources.

The Structure of the Barley Program

The structure of the program (*Figure 1*) reflects the major macroenvironments where barley is grown (Ceccarelli *et al.*, 1987b). The activities of the Aleppo-based program are mostly addressed to the macroenvironments described earlier. The Mexico-based program addresses high elevation areas in a subtropical climate, with Latin America receiving regional priority. Obviously, as different target

environments differ in the pattern of diseases and pests, in crop utilization and farming systems, in availability of inputs, and in agroecological conditions, all these factors affect the strategies being used and the type of germplasm being developed by the different projects.

Objective

The overall objective of the barley breeding program is to develop and disseminate, in collaboration with national programs, improved germplasm and more efficient research methodologies to increase barley production.

Size of the Breeding Program and Methodologies

The total number of crosses is between 1000 and 1200 in the Aleppo projects, and about 1000 in the Mexico-based project. Each year, a number of crosses are made specifically for some national programs. The methods used to manipulate the segregating populations vary depending on the target environment and on the objective of the cross.

The main methods are: (1) a bulk-pedigree method (Ceccarelli & Grando, 1990) for the material targeted for dry areas; (2) the pedigree method for other environments; (3) backcross, mostly for disease resistance; (4) the single-seed descent; and (5) pure-line selection within landraces.

Recently we have developed dihaploid production both through anther culture and *H. bulbosum*, but the amount of breeding material used with these techniques is still limited.

The yield testing before promoting the material to international nurseries is conducted for a period of three years, at the end of which we have information from a minimum of nine environments (years and locations) (Table 3). The experimental designs most commonly used are the lattice (either simple or triple) and the modified augmented design (Lin & Poushinsky, 1983). Plot size in the yield trials is 8 rows at 20 cm with a length of 2.5 or 5.0 m.

The selection criteria used during the testing stages are indicated in Table 4. Most of the traits other than grain yield are the result of the physiology work conducted during the last four cropping seasons (Acevedo & Ceccarelli, 1989).

The data collected during the testing period, together with the data on disease resistance, are used: (1) to select germplasm for the international nurseries; and (2) to evaluate the efficiency of selection in relation to the environment of selection, type

of germplasm, and analytical versus empirical breeding.

International Nurseries

Four types of international nurseries are distributed each year upon request, largely to scientists in developing countries but also, to some extent, to scientists in developed countries (Table 5). The international nurseries distributed at present are: (1) the crossing block (parental lines divided in groups according to specific characters or combinations of characters), (2) the segregating populations (F2 and F3 populations), (3) the barley observation nurseries (new breeding lines generated by the program), and (4) the regional yield trials (a replicated yield trial with the best lines from the observation nurseries). The last three nurseries are divided into three groups specifically designed for low rainfall areas, moderate rainfall areas, and high elevation areas. The nursery for low rainfall areas is further divided into two subsets, one for dry areas with mild winters, and one for dry areas with cold winters. Winter and facultative germplasm with winter hardiness will be distributed, beginning in 1990, as a joint ICARDA/Oregon State University nursery. Special nurseries for specific purposes (such as the heat-tolerant nursery, the grazing nursery, etc.) are assembled and sent only upon request.

One of the most recent developments in the international nurseries has been the use of the barley observation nurseries by other scientists to test their own material in many locations.

The results of the International Nurseries are made available in the form of an *International Nurseries Report* produced each year in June.

Testing of Breeding Strategies

The data collected during the testing period have been used during the last five cropping seasons to attempt to address some methodological issues such as: (1) optimum environment for selection, (2) roles of different types of germplasm, and (3) analytical breeding and drought resistance.

These issues have been considered primarily from the point of view of breeding for unfavourable conditions to provide a methodological framework for national programs.

Optimum Environment for Selection

The question of the optimum environment for selection has been and still is frequently discussed in the literature. The question is particularly important

when, in the target environment, yields are limited by climatic factors which are variable in frequency, timing, intensity, and duration.

A recent analysis of two sets of barley genotypes, each evaluated for three cropping seasons (1986-88 and 1987-89) in contrasting environments (Ceccarelli & Grando, 1991), indicates that the material selected under stress conditions has a higher grain yield under stress, a lower grain yield under non-stress, and a lower average grain yield than the material selected under non-stress (*Table 5*). The analysis of the selection history of the breeding materials outyielding the best checks (*Table 6*) indicates that: (1) selection under non-stress did not generate any line outyielding the best check under stress, and (2) about one-quarter of the lines selected for grain yield under stress outyielded the best check under stress. Among the material outyielding the best check under stress, landraces were 1.6 times more frequent than improved germplasm (*Table 7*). Improved germplasm and landraces appear to achieve the same levels of grain yield under stress through different mechanisms, as indicated by the different heading time, probably related to drought-escape and drought-resistance/tolerance, respectively. The consequence is a significant difference in grain yield under non-stress conditions.

From these and other similar results (Ceccarelli, 1986, 1987; Ceccarelli *et al.*, 1987c; Ceccarelli, 1989), we concluded, at least for the type of stress environment we use for our testing, that: (1) it is possible to identify consistent and repeatable genetic differences under unfavourable environmental conditions only if selection is conducted under the variable conditions typical of these environments; (2) yield potential, or even yield under suboptimal conditions, is not an efficient selection criterion to identify superior genotypes for unfavourable conditions; and (3) selection under stress does not necessarily reduce yield potential. The tradeoff between yield potential and yield under stress varies with the crop and with our definition of stress.

There is a body of experimental evidence (see for example Atlin & Frey, 1989, and Nageswara Rao *et al.*, 1989) confirming these results and suggesting the need for separate breeding programs for favourable and unfavourable conditions.

Based on this evidence, the strategy followed by the barley breeding project is to select genotypes for their stability of performance within a given macro-environment irrespective of their performance across macroenvironments (Ceccarelli, 1989). The rationale

for this strategy is that in unfavourable environments, the probability for the full expression of yield potential is very small, and therefore yield stability has the highest priority.

Recognizing and accepting the principle that genotypic differences can be exploited under unfavourable conditions has important consequences related to sustainability, such as the following:

- ▶ A larger number of varieties will be grown at any moment in time rather than the very few, often closely related, which have made possible large yield increases in favourable conditions. This is because stress environments often differ largely in the predominant stress factor.
- ▶ Utilization of plant genetic resources such as landraces and wild relatives in crop improvement programs: It is unlikely that this type of germplasm can contribute more than a few genes to improve production in high input agriculture and in favourable environments. However, in unfavourable environments where the strategy of improving production by a different partitioning of the biomass has not been successful and is not necessarily sustainable, the incorporation of landraces and wild relatives in breeding programs has already proved to be a valuable tool. This is illustrated by the performance of Tadmor, a pure line selected from the Syrian landrace, A. Aswad (*Figure 2*). Tadmor has shown a yield advantage of 6% over the landrace, an average of four cropping seasons and 26 locations, and a similar coefficient of variation within and between seasons.

The analysis of grain yield under dry conditions in the breeding material classified according to common parents has also indicated differences associated with some specific genotypes. This information is being used to generate random inbred lines for RFLP or DNA fingerprinting to investigate the possibility of using, in the near future, marker assisted selection for grain yield under drought.

Type of Germplasm

Among the alternatives in the type of germplasm which could be used in plant improvement programs, three specifically relate to ICARDA's plant improvement work: (1) high input or low input varieties, (2) genetic uniformity or genetic variability, and (3) conventional versus less conventional (landraces and wild progenitors) germplasm.

High input or low input varieties. This alternative is conceptually similar to the optimum

environment for selection. The transfer of high input varieties into a low input environment has been largely unsuccessful and, even in the more favourable environments of developing countries, there is now evidence of declining yields in spite of high adoption rates of improved varieties and high investment in irrigation and fertilizer. In contrast, there is alarmingly increasing evidence of the environmental damage that can be caused by an agricultural development based on the continued heavy use of inputs. Such damage ranges from direct effects on the environment to depletion of both physical and biological resources.

In more marginal areas, particularly in the dry areas, gains have been relatively modest, and there is a widespread belief that big breakthroughs are going to come more through crop management and resource management than by breeding. While there are few doubts that both crop management and resource management can increase yields and preserve physical and biological resources, the role of breeding seldom has been put in the correct context. It is our opinion that two points must be recognized to assess properly the role of breeding in unfavourable environments:

- ▶ Breeding for unfavourable (climatically or agronomically or both) environments has been based on the assumption that increases in yield potential would automatically generate, as a "residual effect," increases in yield under stress conditions. We have already seen that it is indeed possible to identify and exploit genetic differences under stress conditions.
- ▶ Many scientists in developing countries have been trained on this concept and, even now, in many research stations within and beyond WANA, a regrettably impressive amount of crop improvement work is conducted under optimum growing conditions.

The combination of these two factors has generated a great deal of skepticism concerning what breeding can do in unfavourable conditions.

The introduction of inputs such as fertilizer and irrigation to create an improved agronomic environment is believed to be an essential prerequisite for successful breeding work (Austin, 1989). However, breeding for an agronomically improved environment might dictate the type of germplasm which will best exploit the "improved agronomic environment." This is likely to be largely based on genetic uniformity, which is the opposite of that biological diversity that is the key element in most natural systems to minimize risk (Wilkes, 1989).

Genetic uniformity or genetic variability. The crops which now sustain mankind in the Middle East and North Africa were among the first domesticates. Their adaptation to the fragile farming systems of dry areas is the product of centuries of natural selection. The components of this close adaptation are, or should be, instructive to plant breeders trying to replace them with improved cultivars. An important activity of barley breeding at ICARDA has been to study the landraces adapted to dry and variable conditions to learn a lesson that a breeder could use in formulating strategies for unfavourable and variable environments (Ceccarelli, 1984; Ceccarelli & Mekni, 1985). One of the most important lessons we have learned is the within-population variation existing within landraces (Ceccarelli *et al.*, 1987a; van Leur *et al.*, 1989). Additional evidence is presented at this symposium by McGee and Grando. After learning such a lesson, it was obvious that we start asking ourselves whether genetically uniform germplasm is the best strategy for variable and unfavourable environments.

A second question that we started asking ourselves a few years ago is whether, in addition to population buffering (heterogeneity), individual buffering (heterozygosity) might also play a role in stabilizing the productivity of landraces. We have started to investigate the amount of cross-pollination in different barley germplasm (improved cultivars, landraces, and *Hordeum spontaneum*). Furthermore, the second phase of the collaboration between ICARDA and Montana State University will include the role of a possible limited amount of heterozygosity in the complex population structure of landraces.

Role of Analytical Breeding

The analytical approach in crop improvement stems from the difficulties of relating genotype and phenotype for complex traits such as yield. These difficulties become even greater in environments characterized by unpredictable variability in the frequency, timing, and severity of a number of physical stresses.

This justifies that in the last 30 years a number of studies have been conducted with the purpose of identifying traits — morphological, physiological, or biochemical — to be used as additional or alternative selection criteria in breeding for stress conditions.

The ideal trait should satisfy the following requirements: (1) be causally related to yield under stress conditions; (2) exhibit genetic variation; (3) be highly heritable; (4) be easy, cheap, and quick to screen; and (5) be able to determine correlated

responses in yield under stress when modified by selection. An additional requirement, often implicit in what has been called the analytical approach (Fischer, 1981), is that the ideal trait should not decrease yield in better environments (Richards, 1982). This requirement is not considered as important in stress environments as the increase in stability of yields defined as a reduction of crop failures:

(1) because the acceptance of very low levels of risk is the most likely strategy of the subsistence farmers (Nix, 1982); and (2) because of the fluctuation of prices, which are usually high in poor years and which make excess production in good years virtually worthless (Marshall, 1987).

Many morphological, physiological, and biochemical traits have been proposed in the last 30 years as indirect selection criteria to improve yield under stress. Some of these characters, based on conceptual models for winter cereals grown in Mediterranean environments developed by Passioura (1977), Fischer (1979, 1981), and Turner and Nicolas (1987), are given in Table 8.

In many of these studies, an estimation of the heritability of the trait and of the causal relationship of the trait to yield under drought conditions has not been made to the extent needed to prove to the breeder the worth of the trait (Clarke, 1987). Hence the conclusion that "too much has been written about putative traits for drought resistance in crops, supported by too little analysis of their actual value as opposed to their potential value" (Ludlow & Muchow, 1988).

However, it still needs to be demonstrated how useful those characters that have been effective in some situations are in a range of situations. One of the reasons for the limited success of the analytical approach lies in the ever-present temptation to find simple answers to complex problems.

When we refer to unfavourable conditions, we are very often referring to conditions that are unfavourable to a varying degree, at different times of crop growth, and for a variable period of time. It is that variability of adverse conditions that is the real challenge, and not the adverse conditions *per se*. This explains why occasionally a single, relatively simple trait has been found to be associated with performance under a given set of unfavourable conditions, and why, under a different set of unfavourable conditions, a different character becomes the key to superior performance. It is relatively easy to identify superior genotypes under the stress conditions of any given year in any given site (the "one-year winners"),

while it is much more difficult to identify genotypes which maintain their superiority across seasons even in one environment. As an example of how different traits can interact in determining the performance of the crop under the variable conditions of stress environments, we have used the four traits listed in Table 9. Although the combinations of traits in Table 9 are certainly oversimplifications, they indicate that stability of yields in unpredictably stressed environments can be achieved with different combinations of traits. Furthermore, within these combinations, the role of individual traits changes with the type, the intensity, and the timing of the stress. Therefore, the search for one or more single trait(s) to cope with variable and unfavourable environments could continue to be disappointing, with the only possible exception of those which are of a highly integrative nature, such as C-13 discrimination.

To test the effect of different architectures of traits, we are presently conducting a selection experiment for different combinations of traits with the objective of selecting for all possible recombinants between the opposite expressions of the traits under investigation and to evaluate their yield under drought (Ceccarelli *et al.*, 1991).

The lesson learned from landraces has been instructive also in formulating our strategies in relation to analytical breeding. If the genetic structure of the landraces is considered an evolutionary solution to survival and performance under arid and semi-arid conditions (Schulze, 1988), then it appears that during millennia of cultivation under adverse conditions, natural and artificial selection have not been able to identify either an individual genotype possessing "a trait" associated with its superior performance or an individual genotype with a specific architecture of different traits. On the contrary, the combined effects of natural and artificial selection have led to an architecture of genotypes representing different combinations of traits. These populations can be extremely useful for understanding mechanisms enhancing stability in stress environments, not only from the genetic structure point of view, but also from the point of view of understanding the adaptive role of given traits. In fact, although variable, landraces grown in environments characterized by a high frequency of stress conditions tend to present a high frequency of specific traits (Ceccarelli *et al.*, 1991).

We may expect, therefore, that the landraces will eventually provide the breeder with yet another lesson on the nature of "drought resistance." It will not be surprising to find that, defined in terms of yield

under stress, "drought resistance" is a genetic abstraction.

Resistance to Pests and Diseases

Pests

Extensive pesticide use has resulted in a number of environmental and health problems in many countries. Because of the potential adverse impact of chemical pesticides on the fragile ecosystems of rainfed areas, ICARDA's objective is to develop integrated pest management strategies for the region's major insect pests. All available control techniques would be combined into a holistic management program that prevents economically serious pest damage to the crop and minimizes environmental hazards. Within the framework of germplasm development, ICARDA's pest management projects have stressed the use of genetic resistance to insect pests and diseases, but always within an integrated pest management perspective. Other control methods, especially biological and chemical control, are researched where genetic resistance/tolerance is shown ineffective.

In barley, wheat stem sawflies, sunn pest, Hessian fly, and aphids are the major insect pests throughout WANA. Wheat stem sawfly and Hessian fly are best controlled by the use of resistant varieties.

Varieties with resistance to these two major pests are also under joint development by entomologists and breeders, as are activities designed to locate sources of Hessian fly and sawfly resistance in barley. Similarly, research is presently conducted in cooperation with NARS in Egypt, Sudan, and Ethiopia to develop barley lines with tolerance or resistance to three of the major aphid pests of the Nile Valley and North Africa. These are *Rhopalosiphum padi*, *Schizaphis graminum*, and *Diuraphis noxia* (RWA). Barley seedlings are tested in a laboratory located at Giza, Egypt, for *R. padi* and *S. graminum* resistance/tolerance. They are further tested in plastic house trials at ICARDA and in the field in upper Egypt and in Sudan before being included in germplasm pools available to breeders seeking aphid resistant/tolerant germplasm.

Work on *Diuraphis noxia* is not quite so developed as for the other aphid species. Recent acquisition of potentially resistant barleys from USDA workers in Oklahoma is the first step in developing germplasm for use within the RWA hotspots of the region, namely Ethiopia, Yemen Arab Republic, and Algeria. In addition to resistant varieties for RWA, we try to

identify and collect parasites and predators for release in RWA-infested areas of the world. RWA cultures are maintained at ICARDA for germplasm screening purposes and to rear locally collected parasites prior to shipping them to centrally located rearing and distribution centers in Paris, France, and Texas, USA. The ultimate goal of these activities is to provide national programs with expertise, international contacts, and germplasm and effective and safe exotic parasites as they become available from laboratories at ICARDA and from other institutions.

Diseases

Within the regions of WANA where cereals are cultivated under rainfed conditions, controlling diseases by chemicals is economically feasible only on a limited scale. However, genes for resistance are available for all major cereal pathogens and can provide the farmer with disease control without additional costs to him or the environment. Traditional farming systems are characterized by low fertilizer inputs and by the practicing of fallow. These, and the large diversity within and between crops, made traditional farming systems less prone to attacks by most plant pathogenic fungi. Cultivation of large areas with homogeneous varieties, a characteristic of modern farming systems, may lead to selection of highly virulent pathogen strains and the breakdown of resistance. A rapid replacement by varieties with new, effective genes for resistance is only ensured within a system with strong breeding, pathology and seed production programs, and an active extension service — a situation that is not present within most developing countries.

In order to aid the sustainability of disease control by genetic means, research should focus on ways to use resistance in a manner that ensures its durability. Our research on barley landraces from Syria and Jordan showed a high level of diversity for resistance to major barley diseases and other characteristics, both within and between collection sites (van Leur *et al.*, 1989). Ongoing studies on some landrace lines with high resistance to barley scald (*Rhynchosporium secalis*) indicate that the resistance is based on a number of genes and therefore likely to be of a durable nature. As this type of germplasm is already adapted to the target area, it can be used as a donor for disease resistance in a crossing program without losing the desirable polygenic nature of its resistance.

An important part of the pathology research in ICARDA is carried out in cooperation with institutions

in and outside the WANA region. Newly developed germplasm from breeding projects in ICARDA and from the NARS is tested through a network of collaborators. National centers with an expertise in specific diseases are taking a regional responsibility in the research on resistance and virulence. Through this research and through collaboration with pathologists in Europe and the USA, a better understanding of the genetic basis of disease resistance and the epidemiology of cereal pathogens will be acquired, which will be used to maintain adequate disease resistance in new cereal varieties.

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TABLE 1. Barley area (million hectares), production (1000 metric tonnes), and yield (t/ha) in developing countries and the world between 1986 and 1988.

	Area (mil. ha)	Production (000 mt)	Yield (kg/ha)
Developed countries	59972	152026	2535
Developing countries	17860	25477	1427
World	77832	177503	2281

SOURCE: FAO, 1988.

TABLE 2. LDC countries with the largest barley areas between 1986 and 1988.

Country	Area (mil. ha)	Production (000 mt)	Yield (kg/ha)
Turkey	3314	7133	2153
Morocco	2446	2869	1173
Iran	2200*	2500*	1136
Syria	1654	1509	913
India	1247	1741	1396
Iraq	1243	1013	815
Algeria	1107	820	740
China	1027*	2773	1701
Total % of LDC	14238 79.7	20358 79.9	1430

*F = estimated. (In the case of China, the actual barley area is close to 3 million hectares.)

SOURCE: FAO, 1988.

TABLE 3. Yield testing in the barley breeding program at ICARDA.

TRIALS	No. of lines	Locations	Rainfall
INITIAL	1600-2000	Tel Hadya Bouider	(350 mm) (200 mm)
PRELIMINARY	600-760	Tel Hadya Bouider	
ADVANCED	240-300	Tel Hadya Breda Bouider Athalassa Terbol	(250 mm) (400 mm) (600 mm)

TABLE 4. Main selection criteria used during yield testing in the barley breeding program at ICARDA.

EMPIRICAL (70%)	Grain yield under stress Grain yield under favourable conditions Grain yield under both stress & fav. conds.
ANALYTICAL (30%)	Earliness Early vigour (5-6 leaves) Ground cover (5-6 leaves) Prostrate habit Plant height under drought Cold tolerance (-10°C)

TABLE 5. Grain yield under stress (YS), grain yield under non-stress (YNS), and average grain yield (Y) of barley breeding materials classified according to the selection environment.

SELECTION ENVIRONMENT		N*	———— (kg/ha) ————		
Year 1	Year 2		YS	YNS	Y
1986 - 1988					
Stress	Stress	108	855 a	4643 c	2904 b
Non-stress	Non-stress	10	522 c	5420 a	3084 a
1987 - 1989					
Stress	Stress	30	781 a	5.78 b	2631 a
Non-stress	Non-stress	32	396 c	5719 a	2454 b

*Number of breeding lines.

SOURCE: Modified from Ceccarelli & Grando, 1991.

TABLE 7. Grain yield under stress (YS), grain yield under non-stress (YNS), average grain yield (Y) in kg/ha, and days to heading (DH) of the lines outyielding the best checks* classified according to the type of germplasm (1987-1989).

TYPE OF GERMPASM	N	%**	YS	YNS	Y	DH
> A. ASWAD (YS)						
Improved	15	1.2	986	5514	2565	118.8
Landraces	12	2.1	942	4161	2530	123.6
> RIHANE-03 (YNS)						
Improved	56	5.6	595	6095	2711	120.8
Landraces	6	1.4	689	5795	3152	119.0
I.s.d. (.05)			217	711	245	2.4

*A. Aswad for YS; Rihane-03 for YNS.

**Percent over the number of entries in different germplasm types in the original population.

SOURCE: Modified from Ceccarelli & Grando, 1991.

TABLE 6. Selection history of the breeding material tested during 1986-1988 and 1987-1989, and outyielding the best checks* for yield under stress (YS) or yield under non-stress (YNS).

SELECTION CRITERIA		Number Selected	No. and % of lines out-yielding A. Aswad				No. and % of lines out-yielding Rihane-03			
Yr 1	Yr 2		N	%	YS	YNS	N	%	YS	YNS
1986 - 1988										
GYS	GYS	108	28	25.9	979	4582	5	4.6	805	5725
GYNS	GYNS	7	0	--	--	--	2	28.6	610	5929
1987 - 1988										
GYS	GYS	30	7	23.3	960	5153	5	33.3	713	5959
GYNS	GYNS	32	0	--	--	--	16	50.0	384	6136

*A. Aswad for YS; Rihane-03 for YNS.

SOURCE: Modified from Ceccarelli & Grando, 1991.

TABLE 8. Attributes expected to lead to improved yield under drought in low rainfall Mediterranean environments.

Purpose	Attribute	Screening tool
Maximize T as fraction of ET	• Fast ground cover • Prostrate growth habit • Good winter growth (early vigor)	Visual Visual Visual
Maximize ET under drought	• High carboxylation efficiency • Low non stomatal effects on NP • Stomatal adjustment to drought • Initial dark followed by light leaf colour	IRGA (C-13 D) IRGA (C-13 D) Porometer crop temp. Visual
Maximize harvest index	• High transloc'n of preanthesis assimilates to the ear • Flowering date • Short grain filling	Desiccation Visual Visual

T = Transpiration, ET = Evapotranspiration; IRGA = Infrared Gas Analyzer; NP = Net Photosynthesis.

SOURCE: Acevedo & Ceccarelli, 1989.

TABLE 9. Examples of hypothetical positive and negative trait* combinations in barley as related to stability** of yield in unpredictably stressed environments.

Geno- type	TRAITS				Yield under terminal stress	
	GV	CT	GH	DH	Cold winters	Warm winters
A	1	3	1	1	-	+
B	1	3	1	2	-	+
C	3	1	3	1	+	+
D	3	1	3	2	+	+
E	1	1	2	1	+	+
F	1	1	2	2	+	+
G	3	3	1	1	-	-

*1 indicates good growth vigour (GV), erect growth habit (GH), early heading (DH), and cold tolerance (CT); 2 indicates intermediate expressions; 3 indicates the expression of each trait opposite to 1.

**+ and - indicate good and poor yield, respectively.

SOURCE: Modified from Ceccarelli *et al.*, 1990.

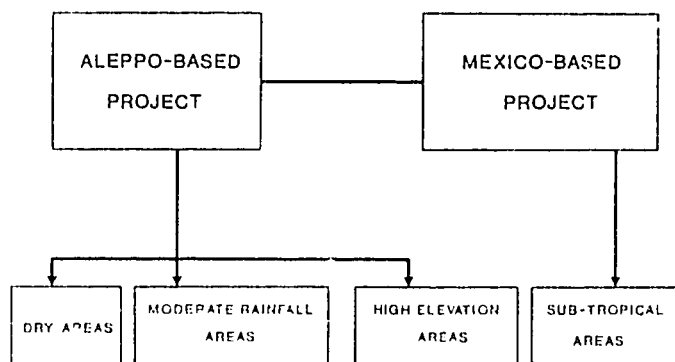


FIGURE 1. The structure of the barley breeding program at ICARDA.

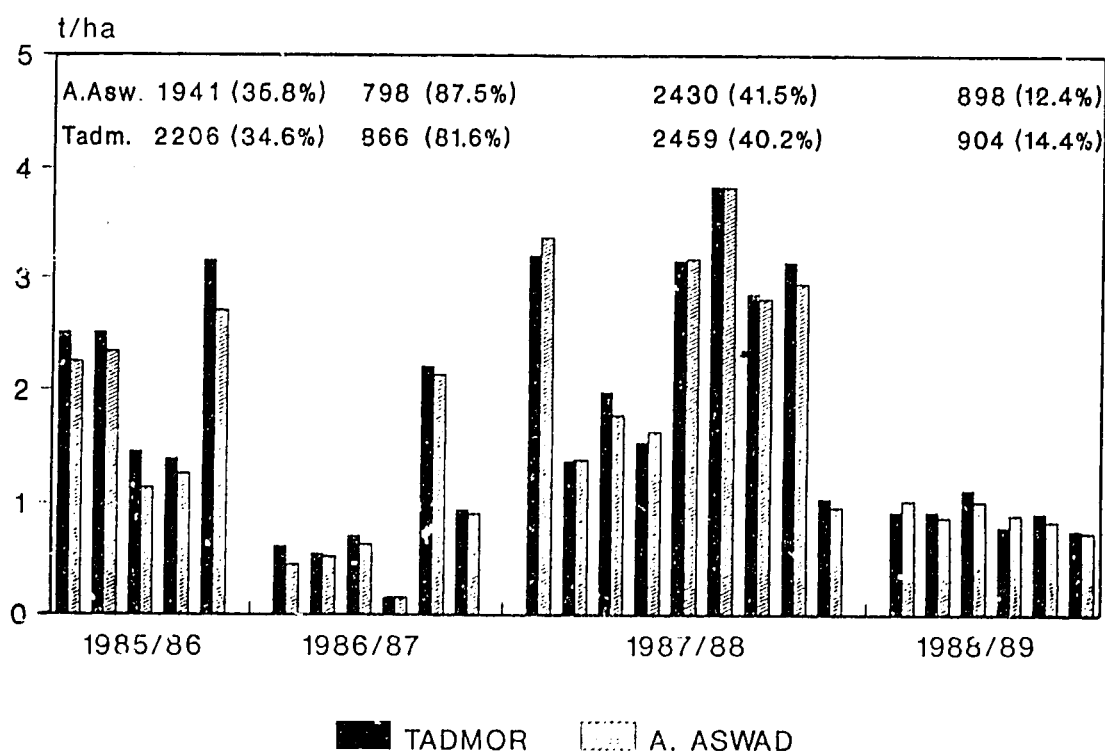


FIGURE 2. Grain yield (t/ha) of a local barley landrace (A. Aswad) and of a pure line selected from A. Aswad (Tadmor) in 26 locations in the driest part of northern Syria. (Average yields in each cropping season and coefficients of variation between locations within each cropping season are shown at top.)

Subsistence Farmer Strategies in Response to Drought and Biotic Stress Uncertainty

Joop A. G. van Leur and Salvatore Ceccarelli*

Summary

Most traditional farming practices used in rainfed barley production in the developing world assist in controlling plant diseases and avoiding abiotic stresses. Improved farming practices are needed to increase barley production. Improved germplasm responsive to new farming practices must be developed to realize full profit from production inputs invested by the farmer. Because better plant development is positively associated with disease development, new germplasm needs greater disease resistance than the landraces presently grown by farmers. However, improved farming practices for rainfed barley will probably not increase yields in the same manner as observed in favourable environments. Abiotic stresses will continue to be the major constraints to yield. Lines may be selected from the local germplasm that have adequate disease resistance and are adapted both to local climate and to improved practices. Most importantly, the use of homogeneous lines should be avoided.

Introduction

Barley domesticated in West Asia has been of primary importance since the advent of settled agriculture. In West Asia and North Africa, barley grain and straw is mainly used as cattle feed. Use of barley grain for human consumption is limited, except in Ethiopia. Barley flour occasionally may be blended with wheat flour in industrial bread making, especially following seasons with poor wheat harvests.

Dryland barley cultivation in the Syrian Arab Republic is hereafter discussed as an example of subsistence farmer strategies. With the exception of mechanized field preparation and harvesting, most farming practices have not changed much over several centuries. Many farmers save their own seed and rarely use fertilizer. The *Annual Agricultural Statistical Abstracts* of the Syrian Ministry of Agriculture record fertilizer use in rainfed barley only since 1986. The 60% increase in barley production realized nationally over the last 20 years was obtained by doubling the total acreage planted to barley (Table 1).

Actual yields decreased over the same period, while those of irrigated and rainfed wheat increased. Decline in barley yields can partly be explained by the unfavourable growing conditions of lands recently brought under cultivation. Drought and cold are the main yield limiting factors causing large variation in yield between years. Because of the high probability of crop failure, farmers hesitate to invest in fertilizer or other inputs that may increase production (Cooper *et al.*, 1988).

Biotic and Abiotic Stresses in Dryland Barley Cultivation in Syria

Abiotic stresses are the main factors limiting dryland barley cultivation in West Asia. Rainfall is unpredictable and variable among years and locations. Cold spells may occur at any time during the growing season, resulting in slow plant growth or in death or sterility if they occur late in the season. Thus, climatic conditions are not optimal for development of leaf pathogens. Still, farmers' fields are rarely free of diseases. Among the leaf pathogens, scald (*Rhynchosporium secalis*) and powdery mildew (*Erysiphe graminis*) may damage yields, especially in areas or seasons with higher rainfall. Net blotch (*Pyrenophora teres*) is usually present, but rarely a problem. First infections of leaf rust (*Puccinia hordei*) usually appear too late in the season to cause significant damage. Yellow rust (*Puccinia striiformis*), although a major disease of bread wheat, was never noticed by the authors on farmers' fields in Syria. Farmers may use fungicides to dress wheat seed, but not barley. Seed-borne diseases are therefore commonly present in barley fields. For example, covered smut (*Ustilago hordei*) is present every year, although its incidence is usually less than 1%. Barley leaf stripe (*Pyrenophora graminea*) may be severe in moderate rainfall areas. Some farmer fields in the

*The International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. (Note: Paper presented at Montana symposium by J.A.G. van Leur.)

moderate rainfall (250-350 mm). Zone of western Syria displayed over 20% striped plants in 1984. Root discoloration can also be observed in most fields, and was recently found to be mainly associated with *Cochliobolus sativus* — one of the causal agents of dryland root rot. The actual importance of root rots in dryland cereal cultivation in Western Asia is not yet known.

Traditional Agronomic Practices and Biotic and Abiotic Stress Factors

Strategies to combat stress factors in low-input farming systems are either based on agronomic practices or on resistance. By examining traditional barley cultivation in Syria, a number of agronomic practices can be identified that assist in the avoidance of both biotic and abiotic stress factors:

Fallow and/or Crop Diversity

The beneficial influence of fallow and the negative effect of monoculture on disease control have been documented (Shipton, 1987). Inoculum of barley diseases, such as scald and net blotch, may pass the summer on stubble. The importance of these and of root diseases will likely increase if monoculture replaces fallow. The same situation occurs for soil and root insect pests, such as ground pearls (*Porphyrophora tritici*) and wheat ground beetle (*Zabrus tenebrioides*) (Miller, 1987). Fallow has a positive effect on crop water availability during the following season. Research at ICARDA has indicated the effect of rotating different crops on soil moisture. In an average rainfall year, traditional lentil varieties do not use all available moisture, leaving some for the succeeding durum wheat crop. New lentil varieties may be bred for higher yield, but if the yield increase is based on higher water use, drought stress on the following crop will be increased (Ceccarelli *et al.*, 1990).

Stubble Management

Barley straw is very valuable in barley-livestock farming systems. In dry years, farmers harvest barley by pulling up plants, leaving little or no plant residue in the field. In wet years or in regions with a high rainfall, stubble is burned to prepare the soil for the summer crop. Both removing and burning stubble lowers the availability of pathogen inoculum in the following season.

Planting Time and Seeding Depth

Some farmers delay seeding until there is enough moisture in the soil for germination and early

plant growth. Late crop development renders the plant less susceptible to frost. Late planting also results in slower development of leaf diseases. Less host material is available during the autumn and early winter, when both moisture and temperature are favourable for disease development. Deep seeding is practiced by farmers who plant before the onset of autumn rains. By the time the seed is moistened, enough water has accumulated in the top soil layers to carry the seedling through dry spells. Local barley varieties lend themselves well to this practice because of their long coleoptiles and varying levels of seed dormancy (Grando, 1986).

Seed Broadcasting

Early ground cover by the crop avoids moisture loss through evapotranspiration (Acevedo & Ceccarelli, 1989). Farmers traditionally broadcast seed using high seed rates. The method used to cover the seed afterwards can affect the rate of ground cover. Unequal distribution of seeding depth, compared to using a seed drill, results in staggered emergence. This could be advantageous if early frost or drought occurs.

Low Use of Fertilizer and Absence of Irrigation

Low-input farming systems have limited yield expectations as well as a low probability of experiencing destructive epidemics. Plant densities are low, while lack of water or nitrogen results in short crop cycles.

Summary

The above mentioned agronomic practices do not constitute deliberate farmer strategies to combat biotic stresses. Farmers are practicing these particular methods to restore soil fertility (fallow), because of lack of funds or an expected insufficient return of investment (fertilizer and irrigation), or because of lack of adequate equipment (seeding time). The only exception might be the burning of stubble. In a recent survey held in northwestern Syria, farmers mentioned control of rodents and insects as a reason to burn crop residues in the field. However, the main reason was actually that it facilitated tillage (Tutwiler *et al.*, 1989).

Traditional Barley Varieties and Biotic and Abiotic Stress Factors

Perhaps the most important factors in the sustainability of traditional farming systems are the local

varieties that were selected over many generations in the presence of the different stress factors. Certain authors recognize that "Landraces will yield something despite biotic and abiotic stress factors, have an excellent general fitness for local conditions and wide spectrum resistance to the diseases in the region" (Harlan, 1976). Others view landraces as disease susceptible and see this characteristic as one of the factors that limit the potential yield (Ruttan, 1989).

ICARDA's barley project began a systematic evaluation of barley landraces from Syria and Jordan in 1984. Single head progenies from a large number of collection sites were evaluated for agronomic characteristics (Ceccarelli *et al.*, 1987) and for disease resistance (van Leur *et al.*, 1989). High diversity in all characteristics studied was found among and within collection sites. Certain characteristics showed differences between regions which could be related to differences in the local environment. Field tests were conducted during the 1989-90 season to investigate local differences with a large number of lines; a total of 25 collection sites, each represented by 20 single head progenies, were evaluated. The collection sites were taken from five regions with distinct environmental characteristics. Winter temperatures decrease from southern Jordan towards northeastern Syria. Rainfall is highest in western Syria and lower towards the centre of the country. A relationship between the environmental conditions of the collection site and the level of disease resistance of the germplasm collected was demonstrated for powdery mildew and scald, but not for covered smut (*Figure 1*). Powdery mildew resistance was more frequent in material collected in the warmer areas of Jordan and southern Syria, where the pathogen is more frequent as well. More scald resistance was found in lines originating from northern Syria. Our survey data show that the scald pathogen occurs more frequently in the northern part of the sampled area. Most striking was that for all diseases a large difference existed among lines within collection sites.

Field tests with mixtures of isolates cannot detect differences in specific resistance genes. Preliminary results of seedling tests under controlled conditions with genetic homogeneous strains of the scald fungus *Rhynchosporium secalis* confirmed the resistance detected with field tests and indicated that the resistance is effective against highly virulent strains (van Leur, unpublished data). From the southern part of the sampled area, landrace lines with resistance to highly virulent powdery mildew strains were identified (Jørgensen, pers. comm.). These results indicate

that the resistance of the Syrian and Jordanian lines to specific diseases is based on a number of genes. However, combined resistance to both scald and powdery mildew is rare (*Table 2*). The negative correlation between scald and mildew scores is caused by the large regional differences and is not significant if the collection sites are analyzed separately. Hence, a careful evaluation of a sufficiently large sample of the local germplasm could yield lines with resistance to both pathogens.

Modern Farming Practices and Disease Development

The growing demand for barley in the developing world can only be met through a higher production per unit area or by expanding the cultivated area. Increasing production by expanding the cultivated area is only possible by abandoning fallow and introducing monoculture. The Syrian government has made plans to abandon fallow; consequently, Syria's barley area expanded to over 2.5 million ha in 1989 (Cooper & Bailey, 1989). This trend can be noticed in different countries and will likely favour disease development, especially of diseases that survive in the soil or on stubble. The increase in cultivated land is not likely to give a sustainable yield increase because of soil degradation, while cultivation of the most marginal zones may become unprofitable due to rising costs of machinery, fuel, and labour. Increasing production per unit area is only possible through improved agronomic practices. Most of these practices are designed to lessen the impact of abiotic stresses. Potential yield may be increased through these methods, but at the same time disease development is promoted by providing more host tissue or by creating a more favourable micro-climate for the pathogen development. The introduction of improved, often exotic, germplasm has been an important part of improved farming system packages in the past. This was necessary in zones with high production potential because local material did not respond to fertilizer or irrigation. The change in the plains of Pakistan from rainfed wheat farming to a high-input system provides an example of the insufficient resistance of old wheat varieties after the creation of a disease-favourable environment (CIMMYT, 1989). However, this new micro-environment threatens the durability of disease resistance, as new pathogen strains with higher levels of virulence can develop rapidly. This process is accelerated by growing large areas of genetically homogeneous varieties, another feature of improved farming systems. Provided that

varieties can be replaced in time, this does not necessarily lead to yield instability (Plucknett *et al.*, 1987). Unfortunately, the infrastructure needed to continuously breed new varieties with different resistance genes and to distribute the seed in a timely manner to the farmers is lacking in most developing countries.

Conclusions

Our results with local germplasm reveal high variability for disease resistance within landraces. We presently don't know how much of this variability contributes to yield stability in general, and to disease control specifically. Resistance of individual landrace lines to specific diseases seems to be based on multi-genes. Local germplasm could be used to develop new germplasm that has both stable performance and adequate resistance, even to the higher disease pressure anticipated in future farming systems. However, the durability of resistance is likely to be increased by maintaining a level of variability in the crop.

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TABLE 1. Yearly average production of wheat and barley in the Syrian Arab Republic during two 5-year periods.*

Period	BARLEY			RAINFED WHEAT			IRRIGATED WHEAT		
	Area	Prod	Yield	Area	Prod	Yield	Area	Prod	Yield
1968-72	701	453	646	1125	844	750	87	132	1517
1983-87	1449	732	505	976	1000	1025	213	604	2836

*Area = 1000 ha; Production = 1000 ton; Yield = kg/ha.

SOURCE: Annual Agricultural Statistical Abstracts, Ministry of Agriculture & Agrarian Reform, Syrian Arab Republic.

TABLE 2. Resistance of 500 landrace lines to scald and powdery mildew.

MILDEW	SCALD		TOTAL
	≤10	>10*	
≤10	14**	126	140
>10	215	145	360
TOTAL	229	271	500

*Percentage leaf area affected, average over 2 replicates.

**Of the 14 lines showing combined resistance to scald and mildew, 2 originate from Jordan and southern Syria, 5 originate from western Syria, and 7 originate from central Syria.

Reaction to powdery mildew of 25 barley landraces, season 1989-90
site averages of first reading for powdery mildew

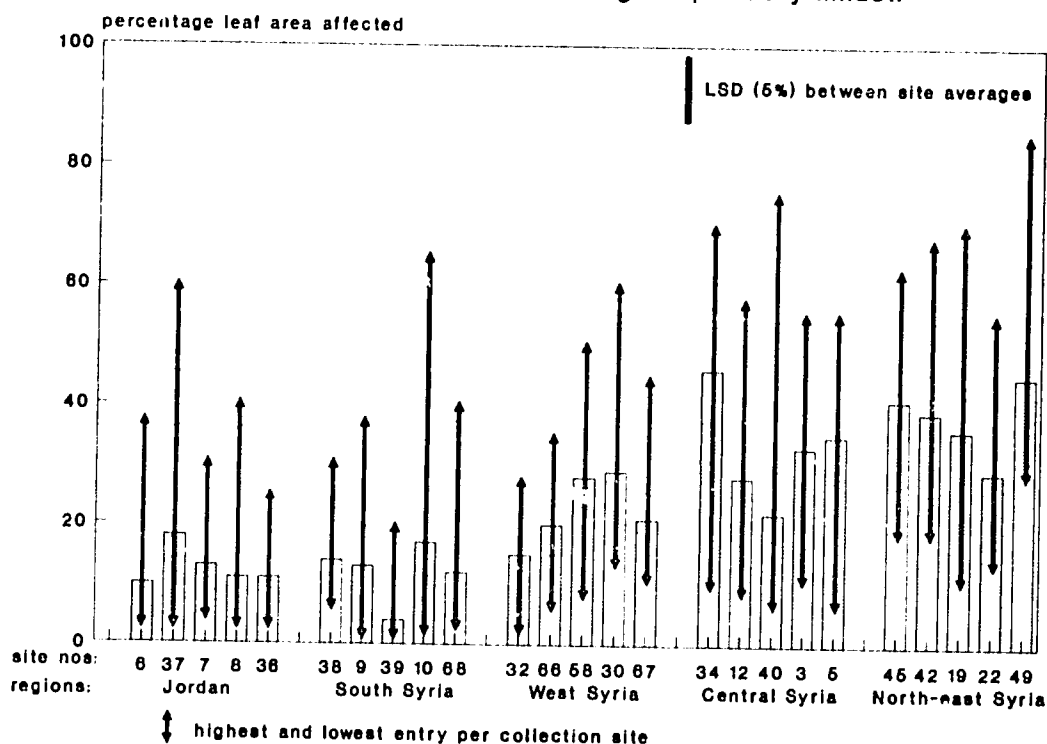


FIGURE 1a

Reaction to scald of 25 barley landraces, season 1989-90
highest, lowest and average reading of 20 lines per site

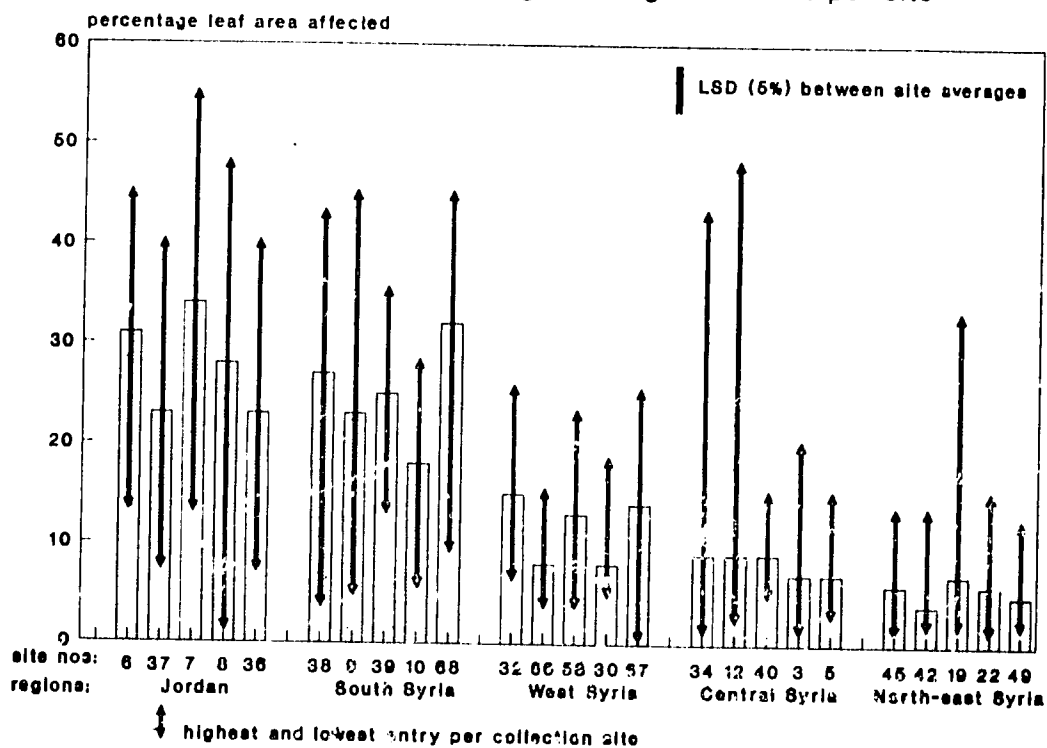


FIGURE 1b

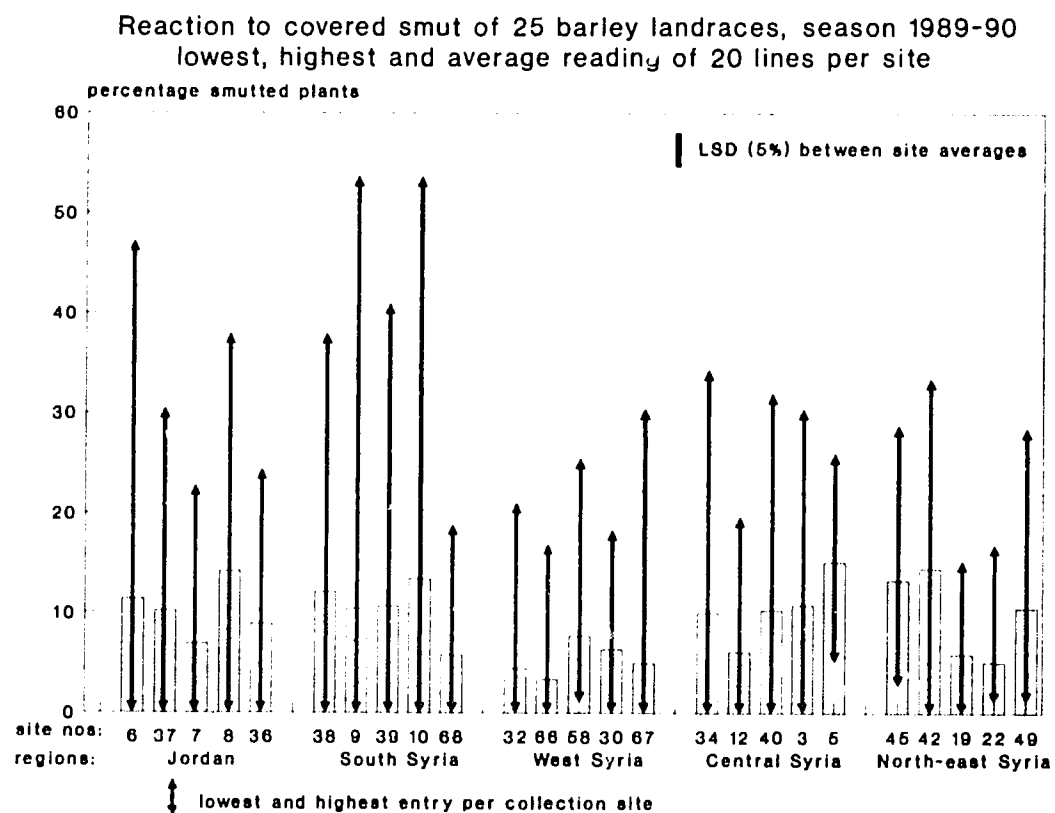


FIGURE 1c

Successes in Transferring Technology Within Developing Countries

Amor H. Yahyaoui*

The general idea of this paper is to develop a comprehensive approach to agricultural technology transfer aimed toward developing countries that offers new alternatives to old and new problems. In a second step, we will focus on successful approaches in transferring technologies within developing countries.

Status of Technology Transfer in Developing Countries

The primary objective of technology transfer in agriculture and the basis for advancing rural development centers on developing local capacities is to generate and adapt agricultural technology to specific farming situations. The farming systems in developing countries are complex in part because of the many physical, biological, economic, and social factors which interact with the total environment. Development of low-input alternatives which lead not only to sustainable food and income, but also to regeneration of the production resource base, is badly needed for the small- and medium-sized farms. This rationale has led developing countries to seek new technologies. To date, the development of technology has essentially bypassed the majority of small farmers who badly need to improve productivity. It is this need which must be addressed by researchers in the development of agricultural technology.

In designing a new technology for small farmers, and especially low-income farmers with limited resources, the key problem seems to lie in adapting appropriate technology that meets their needs, suits their environment, and makes use of the resources available to them. Hence, many of the agricultural research results produced around the world must be tailored to particular local conditions before they can play a role in enhancing food production. Successful agricultural research has supplied farmers with new and improved techniques resulting in large yield increases. Agricultural production world-wide has increased by 60% since the mid-1960s (Anderson, 1989).

Impacts of International Research Programs

International agricultural research centers (IARCs) have played an important role in technology development and transfer. The IARCs were successful in conducting research both on crops and farming systems, in disseminating genetic material and scientific information, and in training scientists. These centers initiated the Green Revolution, a movement in which high yielding varieties of wheat and rice were deployed and disseminated during the 1960s. Nonetheless, critics charge past IARC programs with a lack of appreciation for the ecological and socio-economic environment they were operating in, the exclusion of peasants as both collaborators and beneficiaries, and the promotion of inappropriate technology (Altier, 1984). The limitations IARCs face in an attempt to promote agricultural growth in developing countries are not a consequence of the nature of transfer. Instead, their problems have been related to the type of technology transferred and the research infrastructure of the adopting country. Many developing countries lacked local research programs during the early years of the Green Revolution and could not absorb new technology.

Role of National Research

Although the new efforts of the IARCs have genuinely pursued new approaches, in most cases their technical recommendations are no different than those of the Green Revolution. It is clear that technology transfer follows several processes, but the micro-dynamics involving individual farmers and their communities are highly variable and culture specific. The IARCs generally have a limited capacity to respond to purely local research needs. Their links with national research programs are often tenuous,

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and it is physically impossible for their staff to cover vast expanses of ecologically diverse terrain. Hence, a critical factor in successful technology transfer is through the establishment of a strong local research program that facilitates technology adaption and adoption. Ideally, an effective program of research and extension for the adaption and transfer of technology should be based on (1) the analysis of target farmers' conditions, and (2) the technical alternatives to farmers' current practices which can be successfully adapted to suit local circumstances through on-farm research. In this respect, we have to recognize that the farmer is not the sole focus of technology transfer efforts; in many cases, agricultural development depends on the availability and operation of certain institutions and infrastructure systems. A major task of the national agricultural development programs, then, is the identification of the major constraints in the process of technology transfer. Their responsibilities should be (1) to diagnose the needs and the production constraints at the farm level, and (2) to develop and adapt technologies for the agro-climatic and socio-economic conditions of the target producers.

New efforts of the IARCs and the international agencies are being deployed to assist national programs in bridging the gap between agricultural research and technology transfer. Recent research programs are geared toward multi-disciplinary approaches that are supported by strong institutional research programs. Among a variety of international research projects, the most successful ones are those involved with farming systems and varietal improvement in field crops.

Farming Systems' Research Impacts

Through the cooperative research programs sponsored by USAID and IARC, farming system research (and particularly on-farm research) has been promoted as a way of developing appropriate technology, and adapting it to specific conditions of target farmers.

Of the new technology that becomes available in a developed nation, that which does find its way into ordinary practices of farmers and villagers is often modified or adapted to local conditions and preferences. Modifications and adaptations are necessary, but the foundation of development should be indigenous. In certain areas, informal field visits that were supplemented with regular events such as field days were used as a mechanism for transferring technology to a large target group of farmers. The

assumption is that improved farming practices spread spontaneously through informal networks of farmers. In some cases, new crop varieties have spread spontaneously among resource farmers (Ewell, 1990). Suitable inputs and management practices to accompany the new crop varieties have also been adapted to local conditions, especially by successful farmers.

Crop Improvement

The predominant model for the generation and transfer of agricultural technology is generally based on systems for breeding in field crops. Appropriate methodologies and practices for the development, testing, and promotion of new technologies based on improved varieties in cereal crops have been established in many developing countries through national research programs and supported by IARC and international financing agencies. In such cases, researchers were able to develop superior genetic material and to implement appropriate production techniques.

Concluding Remarks

International assistance has played a major role in upgrading the level of research within developing countries, mainly through the training of scientists. An important number of qualified researchers are now located in several countries, and are involved in developing appropriate research methodologies and cultural practices for specific local conditions, and hence are contributing to increased crop production. Regional research activities are being developed and adapted within developing countries. An outstanding accomplishment is the establishment of a regional research program in North Africa that deals with cereal and food legume diseases. This program involves researchers from national programs of the Maghreb countries. The project is sponsored by UNDP; it will allow the monitoring of diseases in the area, and hence reduce crop losses.

Thus far, agricultural research has supplied new and improved technologies that have resulted in large yield increases in the major cereal crops. The important technological developments that contributed to this increase in crop production include the use of fertilizers, weed control, high yielding varieties, and improved farm management. The availability of research funds and the training of scientists have both played a major role. New developments in molecular biology, including biotechnology and plant transformation, hold great promise and are expected to boost agricultural production.

Improved and new technologies are expected to lead to increased food production, increased incomes, and the improved well-being of rural people — farmers in particular. The benefits, however, will depend mainly on the speed of transfer and how the technology is actually transferred. Nonetheless, in developing countries, care should be taken to avoid excessive specialization and to increase efforts to optimize the talents and skills of individuals and their organizations. In developing new technology, special attention should be given to the efficient use of scarce resources in traditional farming systems, particularly in the semi-arid regions.

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Where Do We Go From Here? — Future Directions

William R. Furtick*

An Overview of the Symposium

The symposium began with a summary of how the world will need to produce more grains, including barley, to feed a growing population that consumes more meat as incomes rise and that increasingly uses grains for industrial purposes. Agriculture must overcome more difficult challenges to meet this swelling demand for grain. Given little recent gains in biological potential for most crops and rising numbers of biotic and abiotic stresses, it is becoming more difficult to maintain even current levels of productivity. An increasing proportion of agricultural research is channeled into maintenance research to keep up with the losses from biotic stresses — the result of crop intensification, and from abiotic stresses — the result of climate change, environmental degradation, and atmospheric pollution. A further constraint is that productivity increases must come from a largely static land base and water supply.

We also discussed the benefits which accrue to U.S. agriculture from improving the productivity of agriculture in developing countries. These countries are the future growth markets for U.S. agricultural exports as their economies develop. Their economic development is largely dependent on improving the productivity of their agricultural sector.

Several papers outlined global production, distribution, and consumption trends in barley, including malting barley used by the brewing industry. The history of barley production as perhaps the first cultivated crop and its centers of origin were also discussed.

Presentations were made on how technology is transferred through research and extension, and sociological constraints on the development and adaptation of new technologies to fit the needs of individual farmers and farm communities.

Much of the symposium was devoted to the various biotic and abiotic stresses that constrain productivity, the breeding methods used to overcome them, and the limitations on attaining stable resistance to these stresses. Particular attention was given to diseases and, to a lesser extent, insects.

These discussions included use of modeling techniques and the state of high technology, particularly biotechnologies and their future potential.

Another interesting topic of discussion was the future role of mycorrhizae in soil nutrient utilization by barley and the potential for genetic transformations that would make barley resistant to various broad spectrum herbicides.

The symposium closed with talks on the status of the AID-supported Montana State University and ICARDA disease resistance breeding program and the breeding programs of ICARDA and its collaborating national programs. The former topic yielded lively debate and a wide divergence of views on what approaches should be emphasized. However, there was consensus on the urgency in collecting and preserving the genetic resources found in local landraces and wild relatives of barley.

With this Background, Where Do We Go From Here? —

The Need for New Partnerships

The dynamic economic, political, and scientific climate of today is quickly changing the state of world agriculture. The cold war has ended and a global economic system has evolved, one that embraces the agricultural sector. A global agricultural research system has also emerged, but has not yet matured. We are witnessing an explosion of new information and communication technologies, together with new discoveries in cellular biology, chemistry, and computer sciences. Unfortunately, it appears that we are unable to digest this immense volume of information, implement these new technologies, and effectively utilize the global research network because the proper institutions and collaborative arrangements are not in place.

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The key to forming these much needed institutional arrangements is planning. Potential partners need to sit down and clearly identify the parameters from the start. Successful partnerships must be based on mutuality of need, benefits, and contributions, both financial and intellectual. This approach has been the core of the AID-sponsored Collaborative Research Support Projects (CRSPs) already mentioned in this symposium as a model for success. It is therefore proposed that the Montana State University/ICARDA program, also funded by AID, be expanded under this successful model with the expectation of establishing a comprehensive global barley program.

Who Should Be the Partners?

The U.S. participants in this global barley program should include the U.S. Department of Agriculture, appropriate universities, and private sector firms conducting either direct or indirect research on barley. Western and Eastern Europe, which combined is the world's largest producer of barley, should also contribute research resources from the public and private sectors. Barley research is also conducted in Australia, Canada, Mexico, and China, in addition to many developing countries in the Middle East, North Africa, India, the southern cone in South America, and South Africa. All of these countries and regions have potential participants that can share the benefits of a global barley program. The IARCs, primarily ICARDA, should have a central role.

What Should Be the Major Components of the Program?

The proposed global barley program should include:

- ▶ Germplasm collection, preservation, evaluation, and distribution.
- ▶ Collaborative research on germplasm enhancement, production technologies, and their use in farming systems.
- ▶ Information collection, storage, evaluation, and distribution.
- ▶ Training, both short-term and degree.
- ▶ Human resource enhancement through meetings, study tours, scientist exchanges, and reciprocal sabbaticals.

What Do All the Partners Need?

All barley producing countries, both industrialized and developing, will need sustained access to global germplasm repositories of barley and its wild relatives

in order to adapt varieties to local conditions. Such varieties must have high productivity, yield stability, and resistance to relevant biotic and abiotic stress. These countries will also need ready access to new information and technologies that will strengthen their capacity to provide for their own farmers.

The U.S. and Other Developed Countries

The largest contribution from the developed countries will be the steady flow of new technologies from basic research, including methodology and equipment, in addition to specific inputs and finished products. Developed nations will also have significant input into the process of disseminating information and providing advanced training, both short-term and degree.

The Developing Countries

The developing countries will also make a substantial contribution. They will be the major source of genetic resources. In the long run, as their agricultural economies and research systems evolve, they, too, will contribute new knowledge and products. In the short run, they will need financial assistance, access to information and technologies, and training for their research and extension staff.

IARCs (Primarily ICARDA)

The IARCs would provide the institutional framework for this proposed global program. ICARDA would serve as: (1) the focal point for germplasm collection, storage, evaluation, and distribution; (2) the transfer point for information collection, assimilation, and digestion between the developed and developing countries; and (3) the overall architect and manager of the global barley program. In addition, ICARDA and the other IARCs would use their expertise and resources in training to establish degree programs jointly with universities and scientific staff upgrading through residencies.

Industrialized countries will provide IARCs with easy access to upstream research, methodology, technology, and information to complement their own research, while helping them transfer this package to the NARS which they serve. The NARS will in turn provide access to germplasm, help test enhanced germplasm and new technologies, assist with training, and disseminate information and technologies on a local level.

The Private Sector

Agricultural research investment by the private sector exceeds that in the public sector. This trend is

dramatically changing the climate of agricultural research, particularly in the field of biotechnology. There will be an increasing reliance on the private sector for both finished products and molecular components of plants, in addition to a wide range of methodologies, equipment, and other inputs. Private sector firms will thus play a much larger role in world agricultural development. Therefore, the global barley program must establish partnerships with this sector as well. This linkage will require greater efforts in order to overcome the constraints of proprietary considerations and the sensitivities the developing countries have in collaborating with private sector firms of industrialized countries.

Why It Is Important for the U.S. to Join the Partnership

While the U.S. is a relatively small producer of barley, it is an important export crop in several regions of the country. U.S. research capacity in barley is also relatively small; however, U.S. farmers must have access to the latest technologies and germplasm. Partnerships with much larger barley research efforts would ensure that benefits accrue to U.S. agriculture. U.S. expertise in high technology and higher education would be its primary contribution to the global barley program.

Several trends indicate U.S. barley producers may become much more dependent on foreign sources of technology than in the past. First, the U.S. is moving toward an imbalance in its investment between basic research and mission-oriented research in the public sector. Secondly, the private sector has not made significant investments in barley in comparison with other major crops. The proposed partnership would not only ensure equal access to new technologies for U.S. agriculture, but also provide U.S. researchers and their students the opportunity to participate in the global research system and develop the understanding of the world agriculture they need to compete in today's global marketplace.

The New USDA "Collaborative International Agricultural Research Initiative"

New international partnerships, like the proposed barley program, are becoming increasingly important to many areas of U.S. agriculture. The need for U.S. agriculture to "internationalize" its policies, perspectives, and partnerships has heralded a new proposal by the USDA, entitled "The Collaborative International Agricultural Research Initiative." The objective of this new program is to invest in collaborative international agricultural research and education that would yield mutual benefits. This program would operate in collaboration with AID's efforts in agricultural research. Barley would be an excellent crop to use in a pilot program for this new initiative for several reasons. First, there is a longer history of U.S. involvement in international collaborative research in barley than for most other crops. Second, global efforts in barley research are relatively small and well defined, which would make it easy to coordinate and manage worldwide efforts in this crop. Another good reason is the importance of barley as the world's fourth most important crop, with world production of 168.7 million metric tons (mmt) in 1989.

The Next Steps

The small, joint Montana State University/ICARDA program is distant from the proposed global barley program outlined today; yet, many participants in this symposium would be the partners of tomorrow's global program. Therefore, in closing, a steering committee should be established to explore the feasibility of a much larger, perhaps global barley program, and how it might be accomplished, financed, and managed.